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MAIZ REVENTADOR[1]

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A remarkable kind of maize discovered in western Mexico by Dr. Isabel Kelly seems not to be known to maize experts, nor to have received any published mention, even of the most casual sort. This is certainly owing in part to the fact that with maize, as with other matters, western Mexico tends to be ignored. It may also reflect the fact that even in most of the area where we have studied this variety, a stranger interested in maize might travel for some time without meeting it in the market-place, the granary, or growing in the field.

In most of that area this maize is known as *"maíz reventador"* (literally "exploder corn", i. e. popcorn), so we shall refer to it by that name though in Jiquilpan and elsewhere in Michoacán it is known (if at all) as *"maíz rosquera"*, and this name is current in parts of Jalisco as well. In the region around Purificación, Jalisco, the name *"reventador"* is used, though *"pipitillo"* is also employed, perhaps due to local hybridization with an imported variety of that name (see below). While *maíz reventador* is commonly used as a popcorn it is a completely different thing from the narrow-grained rice popcorns of central Mexico and bears only a general resemblance to the pearl popcorns of commerce.

Maíz reventador is small-grained, small-cobbed, flinty and undented (see fig. 1, table 1, and pls. 15 and 16). It is 12–16-rowed, with grains 6–7 mm. wide and about as high as they are wide. It is characteristically pure white, though red pericarp is well established in some localities. While yellow grains or occasionally all yellow ears are seen, all those which we have submitted to progeny tests showed obvious signs of having been crossed with other kinds of

[1] Much of the work reported in this paper was carried out while the author was a Fellow of the Guggenheim Foundation. Facilities for progeny tests were made available by the California Institute of Technology and by the Blandy Experimental Farm of the University of Virginia. Grateful acknowledgment is made to these institutions, to Prof. Carl Sauer, who provided the material for the initial study, and to Dr. Isabel Kelly, who made most of the actual collections and supplied much critical information. As it stands, the paper is very largely due to her help and advice though she is in no way responsible for its imperfections.

TABLE I

EAR AND KERNEL CHARACTERISTICS FOR COLLECTIONS OF *MAIZ REVENTADOR* AND *MAIZ CHAPOLOTE*

Collection locality	State	Number ears measured	Mid-ear width*	Ear-stalk diameter*	Kernel width*	Kernel thickness*	Row number	Color
Chachahuatlán	Jalisco	25	2.8–3.2–3.7	.7–1.0–1.3	.4–.7–1.0	.3–.3–.4	10–14–16	White
Jiquilpan	Michoacán	25	2.5–3.1–3.6	.5–1.0–1.3	.5–.7–1.0	.3–.3–.4	10–14–16	White
Coalcomán	Michoacán	1	3.3	1.0	.7	.3	14	White
La Huerta	Jalisco	2	3.1	1.2	.5–.7	.3–.4	14–16	White
Tenamaxtlán	Jalisco	3	2.5–2.9–3.1	.7–.9–1.0	.6–.7–.7	.3–.3–.4	10–14–14	White (one red pericarp)
Ayotitlán	Jalisco	4	2.9–3.1–3.5	.9–1.1–1.5	.7–.7–.8	.3–.3–.4	12–14–16	White
Culiacán	Sinaloa	2	2.7	.8–.9	.7–.8	.3–.4	10–12	Tan pericarp

*Where three numbers are given the first is the lowest value in the collection; the next is the average (median); and the last is the highest. All measurements are in centimeters.

maize (see below). The husks are extremely tight and longitudinal compression lines can be seen running more or less the length of the ear, across the face of the kernels. The kernels are in straight rows, but the pairing of the rows is not evident, and since successive kernels in any row usually are of different shapes and frequently of different sizes they may be described as "tesselated" in contradistinction to those kinds of maize in which successive kernels in a row tend to be mechanically uniform in size and in shape.

The plant descriptions which follow are from end-season plants examined at Chachahuatlán, near Tuxcacuesco, Jalisco, Mexico, and from progeny tests grown at the Blandy Experimental Farm of the University of Virginia and at the experimental fields of the California Institute of Technology at Arcadia, California. It is known that many of the characters discussed below are affected by length of day, and it is probable that other factors such as night temperature are also important. This is particularly true of the date of maturing and number of tillers, two characters which are notoriously affected by place and time of planting.

Both at the Blandy Farm and at Cal. Tech. the plants of *maíz reventador* were extreme in their vegetative characters. They had narrower leaves with deeper channels above the midrib and with heavier midribs than any other varieties grown with them or studied previously at these laboratories. They bore more tillers, which were less differentiated from the main stalk, and they were later to mature. In Virginia they were not able to tassel before the growing season was stopped by frost, though other Jaliscan varieties managed to tassel if not to set seed, and maize from the highlands of Michoacán was only a little slower to mature than the local Virginia corn. In California they were later-seasoned than anything else in our cultures, much later than corn from Michoacán and a month later than sweet corn, "*maíz dulce*", from Jalisco.[1] Furthermore, the yellow-grained *maíz reventador*, which was most certainly the result of crossing between white *reventador* and other varieties, was the earliest of these popcorns to mature, some of its plants being only a week later than the Jaliscan sweet corns. In Jalisco most maize is planted so late in the season, due to the dry winter and spring, that tillering is discouraged. However, from the results reported above we know that, given the proper conditions, *maíz reventador* is later-seasoned and has more tillers than any other maize which we have grown in our extensive tests.

The plant color of *maíz reventador* was also extreme, though similar to that of varieties grown by the Papago Indians and their relatives. There was no color on the upper leaves, but more or less of a dark mahogany-red was apparent on the exposed parts of the stem. On the leaves below the node bearing the ear there was no color on the blade except around the auricle, which was quite deeply marked with red on some plants. The sheaths of the lower leaves were evenly (and often brightly) colored with a clear red along the veins, even when they

[1] Kelly, Isabel, and Edgar Anderson. Sweet corn in Jalisco. Ann. Mo. Bot. Gard. 30:405-412. 1943.

were not exposed to strong light. On some plants there was a slight deposit of color between the veins, but even on these plants the superficial aspect was that of red veins on a green background. The silks were uniformly green or a light sun-red that bleached out in the sun and could only be detected on cloudy days. The anthers were green or a very pale sun-red. There was a considerable and variable deposit of dull red on the glumes of the tassel. Five of the progeny tests of collected ears showed a heavy marking of red at the base of the glume (glume bar); one showed only a faint glume bar.

The tassels were long, slender, and wiry with small to average spikelets but very long branches. The lower internodes of the tassel were often extremely long, producing tassels of large size and low density. Most of the plants had 15 to 30 branches but there were a few with "ramosa-type" tassels which lacked a developed central spike and bore many short branches, decreasing in size towards the apex of the tassel.

The plants from the yellow-kerneled ears were similar in all the above characteristics, but were more variable and possessed numerous features characteristic of other kinds of Mexican maize. Some of them had bright red silks and tassels; most of them had a strong development of interveinal color on the sheaths of the upper leaves, and their tassel branch number, while extremely variable, was smaller (table II). As mentioned above, they were earlier-seasoned and had fewer tillers. All of these results would be expected if they were crosses between white *maíz reventador* and yellow Jaliscan sweet corns. Mr. Raymond Baker, who used one of these yellow ears in a cross, reports that sweet kernels segregated out in the second generation, practically proving this assumption.

Most of the variability in our collections of *maíz reventador* seems to be due to crossing with other kinds of maize, such as that just described with *maíz dulce*. Thanks to the interest of Sr. F. Vargas Tentory, we received maize collections from three forest clearings in the Coalcomán area of Michoacán((1) on Map 1). A variety very similar, if not identical, to *maíz reventador* was present in all three clearings, though in two of them it sometimes had a bright red pericarp. In two of the collections there were many obvious intermediates between *maíz reventador* and larger-grained varieties. Similar collections have recently been received from the coast of Michoacán.

Resemblances.—The only variety closely resembling *maíz reventador* which has come to our notice is a series of ears presented by Ing. Taboada of the Dirección General, Secretaría de Agricultura y Fomento, to whom we are indebted for these and other favors. The ears presented by Ing. Taboada came from Culiacán, Sinaloa ((14) Map 1), where they are known as *maíz chapolote*. They are quite similar to *maíz reventador* except that they look even more primitive and have a dark tan pericarp. The plants differ in being much shorter-seasoned. *Maíz reventador* is of particular interest because it is so much like a kind used in western Mexico in the Colonial period (see below). Two archeological occurrences are known, both excavated by Dr. Isabel Kelly, one at Paso Real, Jalisco ((5)

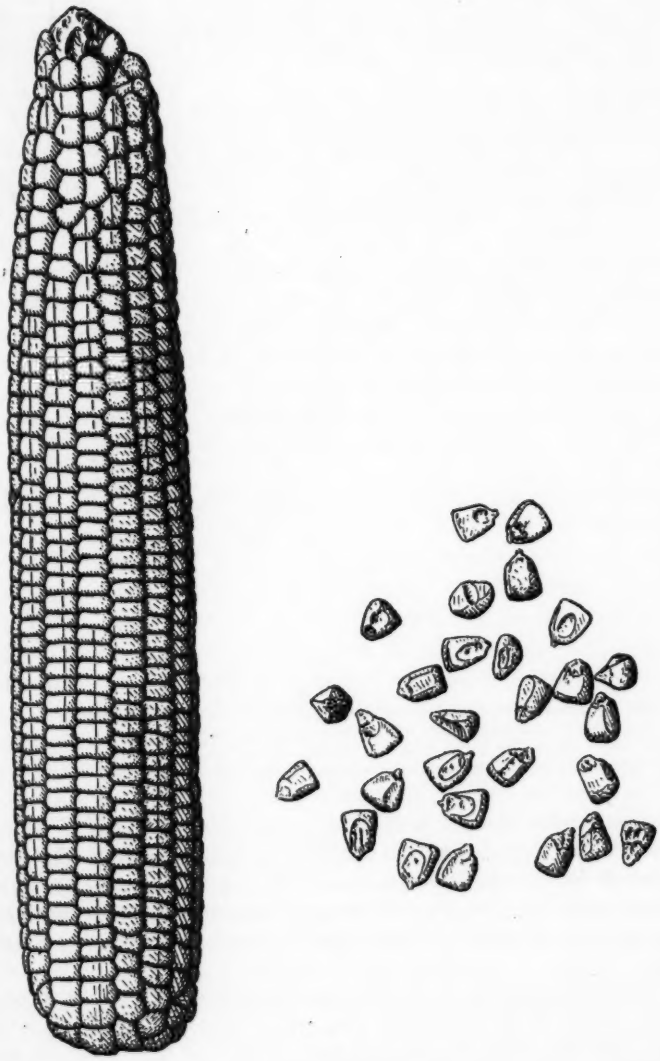

Fig. 1. Ear of *Maíz reventador* from Chachahuatlán, Jalisco, and shelled kernels from the same. Natural size.

Map 1. Distribution of *maíz reventador:* Solid black dots, regions where it is *not* grown and is apparently unknown; open circles, localities where *maíz reventador* or a very similar variety was collected or from which a similar, if not identical, variety is known from archeological investigation or historical documents. See the text (pages 309–311) for further details.

Map 1), on the Rio Armeria, downstream from Tuxcacuesco, and the other from Culiacán, Sinaloa (14). Both are only charred fragments of cobs but these are large enough for us to estimate kernel-size, cob-size, tesselation, and row number. If these charred fragments did not belong to *maíz reventador,* as here described, they must have belonged to some closely related small-cobbed, small-grained variety.

A detailed description of the fragments from Paso Real will be found in an appendix to Dr. Kelly's report on that area. Those from Culiacán were not received until that report was in press and are described here to put the facts on record.

As received for examination from the Museum of Anthropology of the University of California the material consisted of several carbonized cob fragments without kernels. The box bore the specimen number 3-6090, and Mr. Gifford's accompanying letter stated that

it was Dr. Kelly's original number 46, from Culiacán, Sinaloa, Trench 2.

The largest fragment was an entire cross-section of a small cob, apparently from near the base. Since one of the smaller fragments was also basal, apparently at least two cobs were represented in the sample. The fragments were conspicuous by the small size of the spaces for the kernels, being slightly smaller than the smallest previously examined in this laboratory (Haury's material from Ventana Cave). The mid-cob width was 1.5 cm., the cob-kernel width was 2 mm. and the cob-kernel thickness was 2.8 mm. giving a cob-kernel area of 5.6 sq. mm.

The largest fragment is somewhat imperfect on one side and the row number cannot be absolutely determined. It is at least 14 and it might possibly be 18. There is no indication of the ear being elliptical, as in much primitive maize, and from the fragments one would judge the ears to have been cylindrical rather than tapering.

As a whole, the material is similar to that discovered by Dr. Kelly at Paso Real. It apparently was a small-grained flint, probably of the same general type as the small-grained popcorns or flints which are still to be found in western Mexico.

In a number of ways *maíz reventador* is quite similar to the remarkable maize grown by the Pima and Papago Indians, resembling it in plant color, narrow cobs, tesselated seeds, well-developed tillers, and prominent husk striations.

Most of the peculiarities of *maíz reventador* are to be found in an even more exaggerated degree in teosinte *(Euchlaena mexicana)*. This is true of the narrow leaves, the slender stems, the tough roots, the late season, the wiry tassel, and the small seeds. The kernels of *maíz chapolote* from Culiacán are even of the same dark brown as teosinte. Furthermore, this variety has large knobs on every chromosome except No. 10. It would seem as if these western Mexican varieties represent a maximum introgression of teosinte. If so, this must have occurred at some time in the past. While teosinte is not unknown in western Mexico it is now a rarity in the fields where we have studied *maíz reventador*.

In a very general sort of way *maíz reventador* is somewhat similar to the maize varieties commonly grown in Jalisco. All of these varieties (known locally by such names as *maíz criollo, maíz blanco, maíz colimato, maíz humeado,* etc.) have a strong tendency to narrow, irregularly tapering ears, strongly appressed at the base, and to husk striations on the kernels (pl. 16, below). They have the general appearance of crosses between *maíz reventador* and other kinds of corn. To use a phrase employed by certain anthropologists, they probably contain *maíz reventador* "in solution." This assumption is at least partially confirmed when the variation in these varieties is examined plant by plant. If they have indeed resulted from crosses between *maíz reventador* and other kinds of maize, then the amount of *maíz reventador* germ-plasm (as well as its kind) should vary greatly from plant to plant, and we might expect to find occasional plants which have the maximum amount possible in that population ("reëmergents," in the language of the physical anthropologists). Such plants should be very similar to *maíz reventador*. This is actually the case. In almost any corn crib in Autlán or Guadalajara or Ameca one will find occasional ears which show a strong resemblance to *maíz reventador*, much stronger than that of most Jaliscan maize. Much more rarely one may even come across a single ear which is almost within range of variation of *maíz reventador* itself.

TABLE II

TASSEL CHARACTERISTICS OF PLANTS GROWN IN THE UNITED STATES FROM COLLECTIONS OF *MAIZ REVENTADOR*

Collection	Locality	State	Plants raised to maturity	Number tassel branches*	Glume length in mm.	Glume bar	% condensed internodes	% subsessile spikelets
Ears with small white kernels								
K. 1	Sayula	Jalisco	6	13–21–28	9	Heavy	0	0
K. 2	Talpa	Jalisco	7	15–19–36	9	Heavy	0	0
K. 3	Mascota	Jalisco	5	18–26–33†	10	Heavy	0	0
Sa. 22	Ayotitlán	Jalisco	4	23–26–29	10	Faint	0	0
Ears with larger yellow kernels								
K. 4	Talpa	Jalisco	5	12–13–29	12	Heavy	10	100
Sa. 11	Tenamaxtlán	Jalisco	5	15–23–28	11	Heavy	40	40

*In the figures for number of tassel branches the middle represents the average (median) value; the others, the lowest and highest values.
†Excluding one plant with *ramosa* type tassel.

Some of our collections demonstrate the way in which *maíz reventador* tends to become incorporated with new varieties introduced into the region where it is grown. From the Purificación area, for instance, we have collections from Villa Vieja ((7) Map 1) and from La Huerta. They demonstrate an apparent blending of *reventador* and a widely grown Mexican variety known as *pipitillo*. From Villa Vieja we have three ears which were being grown under the name of *pipitillo* and were said to be the common corn of that region. As a whole, they look more like *reventador* than like *pipitillo* as that name is commonly applied in other parts of Mexico (Guanajuato, Michoacán, Mexico, Morélos, etc.). However, as compared with pure *reventador* they are larger-grained, larger-cobbed, and with proportionately longer kernels. On closer inspection one of the ears (pl. 16, extreme left, below) is enough like *pipitillo* so that it might pass under that name in a region such as the Los Altos zone of Jalisco where *pipitillo* is not as extreme in type as it is around Mexico City. It is not only outstanding for the characters enumerated above but it has kernels more or less dented; it has a conspicuous capping of starch and some of the kernels show a slight tendency to pointing (all of these being attributes of *pipitillo*). It would seem as if a genuine *pipitillo*, once introduced into this region, is now so swamped by repeated contamination with the local *reventador* that there are only traces of its original characteristics. This suspicion is confirmed by the collection from La Huerta (pl. 16, above) in the same general region. This consists of four ears, two of which are practically pure *reventador* and two of which have colored aleurone and slightly larger seeds. Significantly, they were identified locally as "*pipitillo (reventador)*".

It seems not unlikely therefore that *maíz reventador*, or at least some very similar variety or varieties, is the foundation stock for the maize of western Mexico and the reason why the maize of that region is so distinctive as a whole. This conclusion is in accord with the archeological information reported above and with the evidence from a colonial document reported in the following section on distribution.

Distribution.—The known distribution of *maíz reventador* (see map 1) lends further weight to the above assumptions. From our own collections we know it to be widespread in western Jalisco, with collections from the Jaliscan plateau and from its southwesterly slopes and fringes. Specimens have been collected at Tenamaxtlán (10)[1], Ayutla (10), Mascota (9), Talpa (8), El Limón (5), and Sayula (6). It is reported by several reliable informants from Ameca (11). We also have collections from Chachahuatlán (5) and Tuxcacuesco (municipality of Tuxcacuesco) (5), from Las Canoas and Ayotitlán (municipality of Autlán) (4), and from Villa Vieja (7), La Huerta and Pueblo Nuevo (Cuautitlán of older maps), all from the municipality of La Purificación as of 1943 (we are informed that this area is being redistricted). We have specimens from the old town of Tlajomulco (12) which are not quite typical and seem to have been mixed with modern commercial pearl popcorn. We have shelled corn sent from

[1] Numbers in parentheses are from Map 1.

Tepic (13), Nayarit, and which was said to be grown near by. We also have specimens from Jiquilpan, Michoacán (2), on the border of Jalisco, and an ununusually reliable informant reports it as fairly common in those parts of Michoacán (3) which are adjacent to LaBarca, Jalisco.

Unfortunately, it is not possible to be as definite about regions where it certainly does not occur (or at least did not occur). In most of the areas studied its occurrence is now so casual that it can be found only after persistent search. In S. P. Tlaquepaque, near Guadalajara, it was not grown during 1943 but it is occasionally grown there, and within the memory of many inhabitants it was regularly grown by a few families. We have not collected it in the Los Altos zone of Jalisco, and several informants from that area did not recognize the name or sample cobs. In Guanajuato we are on firmer ground because of the extensive collections made by Dr. E. Limón of the Campo Agricola Experimental at León. He did not know it and nothing like it was represented in his collections. We are convinced that it does not now occur and has not recently been grown in the highlands of Michoacán (Cherán, San Lorenzo, Pátzcuaro, Uruapan) or in the region of intensive maize culture around Mexico City. In the collections of the Dirección General de Agricultura y Fomento at San Jacinto there are no ears even remotely like it from any of these regions and the specimen ears which we carried were viewed with equal astonishment by farmers, dealers, and agricultural experts. (In Jalisco, on the other hand, they were usually recognized, and the peculiar properties of the variety were described even in those towns where none was being grown in the current year.)

In addition to its general resemblance to west-coast maize one reference suggests that *maíz reventador* was formerly widely distributed northward. In the Biblioteca del Estado in Guadalajara there is a manuscript copy[1] of the 1776 Relación of (San Miguel de) Sahuaripa, (15) map 1, in Sonora, which describes a *maíz "rebentador"* with small white grains and says that in the form of *pinole* it was common provender of the area[2].

We have several times referred to the casual occurrence of *maíz reventador* at present. It may be well to present in detail some of the actual facts on which this statement is based. In Tuxcacuesco (5) it is grown by a single family who pops it and sells popcorn balls locally. At Chachahuatlán several families grow a little of it, usually only one row or part of a row in their *milpa* (yellow *maíz dulce* is often grown in the same incidental way in an adjoining row which accounts for part of the yellow kernels). At Ameca (11) several reliable informants report it as being grown in this same way by a very few families. In

[1] Manuscript No. 50, T. III.

[2] "Ay rebentador que llaman; pequeno el grano, y blanco este porque abunda para pinole que lo asen tostando dicho Maiz y moliendo,[10] y es el Bastimento corriente de la tierra, el qual toman batido en agua fria, lo reserban solo para esto" . . . There is (the kind) called popcorn, with little white grains, for this is abundant. They make pinole of it, toasting the aforesaid maize and grinding it up and it is the regular food stuff of the land, being eaten stirred up in cold water; they reserve it [popcorn] for this alone. [Spelling and punctuation somewhat modernized.]

Jiquilpan, Michoacán (2), two families make a regular practice of selling popcorn balls in the local markets and on the street outside their houses. They grow a little themselves and occasionally buy additional ears. In Tlajomulco (12), in 1943, it was grown by only one family who had 15 or 20 plants along one edge of their corn field.

In questioning informants as to where it might be obtained we have often (Ameca is one exception) met with the statement that more of it was being grown up in the hills (*"en el cerro"*). Questions as to why it was more frequent in the hills met with a variety of answers ("more water", "better soil", "better drainage", etc.). We suspect that if it is indeed commoner in the hills, as has been so frequently reported, it is there because it is an ancient kind of maize and like many other ancient things it survives longest in out-of-the-way places.

Uses.—Maíz reventador is used at the present time for popcorn and for *pinole*, though the latter is made from other varieties of maize as well.[1] Sometimes the popcorn is sold as loose grains, with or without sugar or salt, but more frequently it is made into balls by the addition of *panocha* (crude brown sugar) syrup. These are variously known as *chivitas*, *palomitas*, and *rosqueras* (the names also used in other parts of Mexico when other kinds of maize are use for popping). In Jiquilpan, Michoacán, the unpopped grains are used in the manufacture of thin sweet cakes, locally known as *ponteduro*. This confection can be made with a variety of materials and is usually prepared as loose, sugar-coated grains.[1]

Directly, *maíz reventador* would seem to be of very limited economic importance. As a popcorn it seems to be inferior to modern commercial varieties. Indirectly, however, it may be of great potential importance. Modern maize breeding is now at the point where it is beginning to improve commercial varieties by planned crosses to bring in desirable characters. For such a program *maíz reventador* has a great deal to offer. It has tough stalks and a tough strong root system. The hard-surfaced leaves and stems are resistant to insect attack and it has tight, tough husks which protect the ear. Some of these qualities may prove useful in creating the maize of the future.

SUMMARY

1. Though previously unmentioned in maize literature, *maíz reventador* is widely, if not commonly, grown in western Mexico. Its prevalence in out-of-the-way places, as well as its close resemblance to the charred remains of prehistoric maize from western Mexico, suggests that it was once a staple crop there. Further confirmation for this suggestion is given by the general resemblances of commercial varieties in the west of Mexico to *maíz reventador*, by the appearance of occasional plants which resemble it even more closely, and by the description of the same or a similar maize in a manuscript of 1776.

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[1] Kelly and Anderson. *loc. cit.*

2. *Maíz reventador* is described in detail. It is outstandingly slender, in cob, leaf and stem; it has tough, strong leaves, stems, and roots. Plant color, when strongly developed, is chiefly along the veins of the leaves rather than between them.

3. It is used locally for confections (*pinole* and popcorn balls).

4. Several of its outstanding characteristics make it important in modern maize-breeding programs.

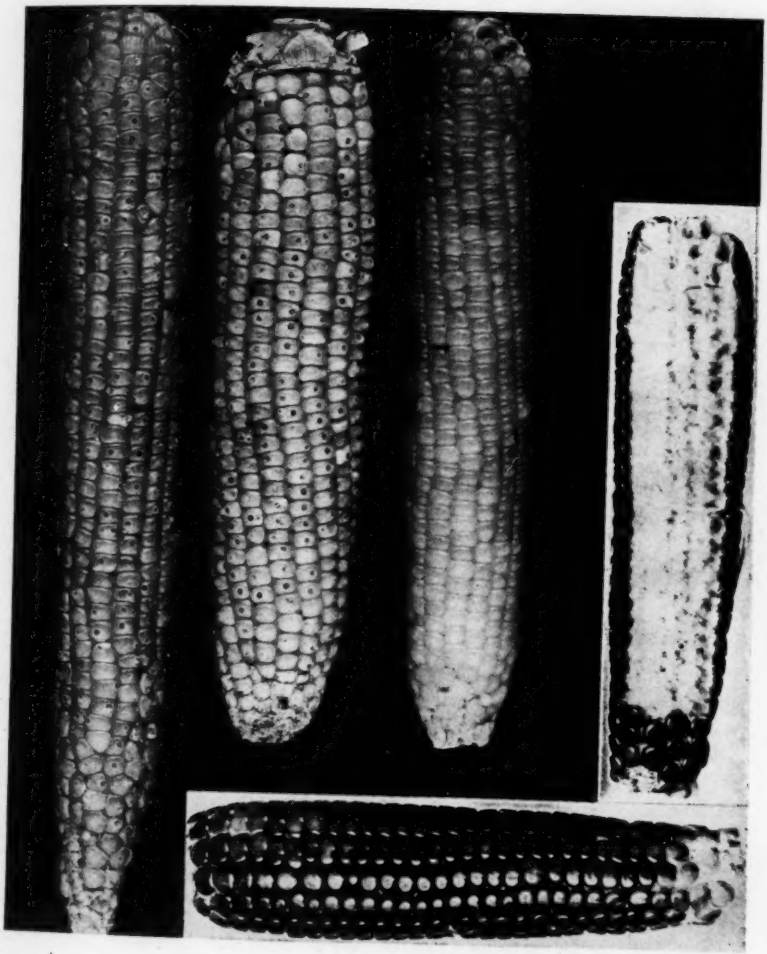
Explanation of Plate

PLATE 15

Three ears of *maíz reventador* and two of *maíz chapolote* (approximately natural size).

Upper left: two ears of *maíz reventador* from Tuxcacuesco, Jalisco (badly damaged by insects), and one from Sayula, Jalisco. Photographs courtesy of the Anthropological Museum of the University of California.

Lower right: two ears of *maíz chapolote* from an *ejido* near Culiacán, Sinaloa, Mexico.



ANDERSON—MAIZ REVENTADOR

Explanation of Plate

PLATE 16

Maíz reventador and other varieties of maize from Jalisco which show probable mixture with it. All ears approximately one-half natural size.

Above, left to right: *maíz reventador* from La Huerta (3 ears), Las Canoas, and Tenamaxtlán (2 ears). The ears from La Huerta were received under the names of *pipitillo (reventador)*, *blanco* and *negro*.

Below, left: Three ears of *maíz pipitillo* from Villa Vieja which are so extensively mixed with *maíz reventador* that only the ear at the extreme left bears any noticeable resemblance to the varieties known by that name in the districts around Guadalajara, Mexico City, or León. See text, page 309.

Below, right: Two ears of other varieties from Jalisco, demonstrating the general resemblance to *maíz reventador* which characterizes the maize of that region. Next to last: *maíz tomateco*, La Huerta. Extreme right: *maíz olatillo*, Ayutla.

ANDERSON—MAIZ REVENTADOR

CYTOLOGICAL OBSERVATIONS ON TRIPSACUM DACTYLOIDES

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Taxonomic work on *Tripsacum*[1] has indicated that *T. dactyloides* is a very complex species. It is composed of at least five different entities, one of which grows in an isolated area in western Texas and has been recognized taxonomically as *T. dactyloides* var. *occidentale* (loc. cit). Aside from this variety, *T. dactyloides* extends from central Texas and northern Kansas eastward to Connecticut and Florida (Map 1). Cytologically, *T. dactyloides* is a polyploid complex and has some races with 18 pairs of chromosomes and others with 36. The cytological work reported below extends the known range of one diploid race into Missouri and Arkansas and suggests that *T. dactyloides* may be exclusively tetraploid along the eastern seaboard.

Materials and Methods.—At the beginning of the project an earnest attempt was made to cultivate the Mexican and Guatemalan species of *Tripsacum* along with a comprehensive collection of the various forms of *T. dactyloides*. After three years of partial success this had to be abandoned as too costly in time and effort. None of these species are winter-hardy in St. Louis, even with careful attention, and even the southern Texas strains of *T. dactyloides* get gradually weaker, and a few die each winter. As a greenhouse plant *Tripsacum* does well in St. Louis during the winter, but it is difficult to bring through the long, hot summer. The collection was kept in fair condition for two years by transplanting to the breeding plot every spring and then putting the plants back into the greenhouse in September. However, when they are treated this way they do not have a regular flowering period, and some of them do not flower at all. A project of this sort could be carried out more efficiently at some such experiment station as La Jolla, California, or College Station, Texas, where the exotic species of the genus are easily grown out of doors. Since *Tripsacum* is a close relative of maize and may even be involved in the history of our cultivated varieties,[2] such a project would seem to be of fundamental importance.

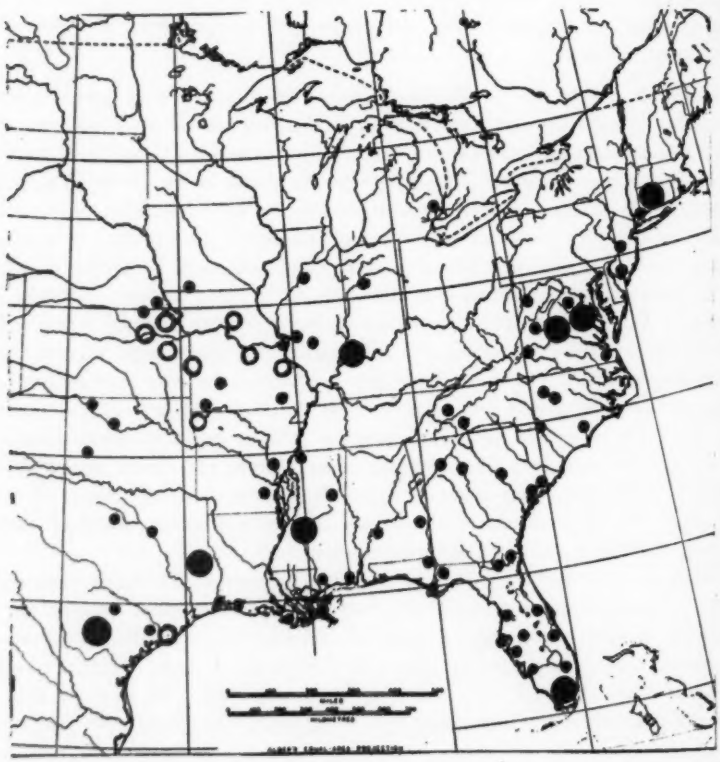
From the more northerly part of its range *Tripsacum dactyloides* was readily grown from seeds or as transplants. Seedlings grew best when planted out of doors and brought in after several weeks of cold weather. Planted out the following spring, they gave good-sized plants by the second summer. In transplanting specimens from the wild, early fall was found to be the most effective time of year and preferable to summer, late fall, or spring. The plants grew well when

[1] Cutler, Hugh C., and Edgar Anderson. A preliminary survey of the genus *Tripsacum*. Ann. Mo. Bot. Gard. 28:249-269. 1941.

[2] Mangelsdorf, Paul C., and R. G. Reeves. The origin of maize. Nat. Acad Sci., Proc. 24:303-312. 1939.

once established, and required only an occasional weeding to keep them in good condition. The following collections have been examined cytologically:

Deam	Collected by Dr. C. C. Deam 7 miles east of Lincoln City, Spencer Co., Ind.	n = 36
Dederick	Plants collected by Leslie Hubricht along stream near Dederick, Vernon Co., Mo.	n = 18
Fourche a du Clos	Plants collected 3 miles north of Bloomsdale, Ste. Genevieve Co., Mo., by Leslie Hubricht.	n = 18
Rivanna	Plants collected 3 miles north of Charlottesville, Va., and studied at the Blandy Experimental Farm of the University of Virginia.	n = 36
Rogers	Seeds collected at Rogers, Benton Co., Ark., by the Soil Conservation Service.	n = 18
Rosebud	Plants collected along roadside 13 miles n. w. of Rosebud, Gasconade Co., Mo., by Leslie Hubricht.	n = 18



Map 1. Distribution of *Tripsacum dactyloides* (exclusive of var. *occidentale*): small black dots indicate herbarium records; large black dots, 2n = 72; open circles, 2n = 36. This map summarizes the previously published information, the counts reported below, and unpublished information kindly supplied by Drs. L. R. Randolph and A. E. Longley, of the U. S. Dept. Agr.

Developing inflorescences were pickled in one part glacial acetic acid and two parts absolute alcohol, and the young anthers were smeared in Belling's aceto-carmine the next day or as soon as convenient, following McClintock's directions as to ultra-clean slides and the gentle use of heat to spread the cells. *Tripsacum* gives the appearance of going through the reduction division at a later stage in the ontogeny of the inflorescence than does maize. Secondary inflorescences pickled just after the terminal florets were clearly visible above the enclosing sheaths were found in every instance to contain pollen mother cells in all stages from early prophase to metaphase. At metaphase the PMC is so elongated that nearly all the cells lie on their sides when smeared; polar views in which the chromosomes can be counted are seldom met with. It was found more practicable to make chromosome counts in diakinesis when the chromosome pairs are showing maximum repulsion. By studying this stage it was also possible to find cells in which an approximate notion of chiasma frequencies and positions could be obtained.

Results.—Chromosome numbers have been enumerated above, with the information as to where the plants were collected. Camera-lucida drawings are shown in fig. 1. In Map 1, the distribution of these plants is shown graphically along with that of those studied by Longley[3], by Mangelsdorf and Reeves[4], and with information graciously furnished by Dr. L. R. Randolph. Taken with the morphological data reported by Cutler and Anderson, Map 1 suggests that the varieties along the eastern seaboard are amphiploid ($n = 36$) and that there is a fairly widespread race ($n = 18$) of lower ploidy along the eastern edge of the Great Plains and in the adjacent prairies. Nothing is known cytologically about the peculiar Tripsacums reported from central Illinois,[5] and the situation in Texas seems to be complex with counts of both $2n = 72$ and $2n = 36$ in the eastern part of the state. More field work in this area would be desirable but the changes wrought in the east Texas landscape by a century of intensive cultivation are so considerable that it might be very difficult, or even impossible, to determine the original relationships of these entities.

As in the related genus *Zea*, the chromosomes of *Tripsacum* undergo extreme contraction between pachytene and metaphase. Chiasma frequencies cannot be accurately determined, particularly at the later stages. At diakinesis it is often possible to make out chiasma frequency with a fair degree of objectivity, for some of the bivalents in a cell. Only very rarely are there cells in which the total frequency can be obtained. Figure 1 (above) shows a camera-lucida drawing of such a cell. The numbers given are minima; the actual total frequency might possibly be somewhat higher; it could not conceivably be any less. It gives an average frequency of just a little over two chiasmata per bivalent.

[3] Longley, Albert E. Chromosomes in maize and maize relatives. Jour. Agr. Res. 28:673-687. 1924.
[4] *loc. cit.*
[5] Cutler and Anderson, *loc. cit.*

In the 18-paired Tripsacums no multivalent associations were recognized and there were no irregularities at metaphase. Frequently one or two bivalents would still be dividing after all the others had divided and moved to the poles, as previously described by Reeves and Mangelsdorf. When carefully examined such cells were always found to be perfectly regular in every other way and the tardy bivalents were symmetrical and were normally aligned upon the plate. It seems likely that they represent some of the larger and longer chromosomes, since it is

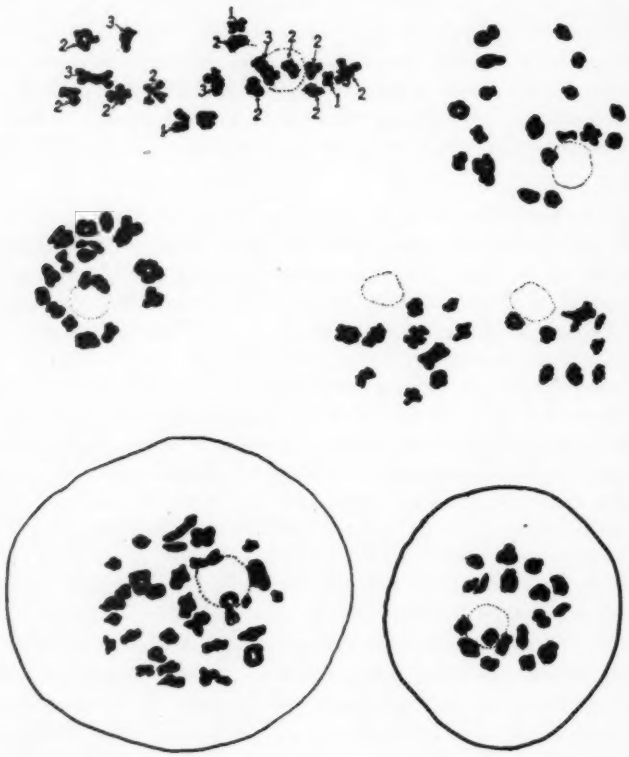


Fig. 1. Camera-lucida drawings (all to same scale) of aceto-carmine smears of *Tripsacum dactyloides* pollen mother cells at diakinesis. Nucleoli represented by light stippled outlines. All show 18 bivalents except the lower left, which has 7 quadrivalents and 28 bivalents. Upper right, plant from Rosebud, Mo.; upper left, PMC from same smear drawn at a slightly earlier stage when the chiasmata are more clearly evident, (Numbers refer to estimated numbers of chiasmata for each bivalent; configurations which would have overlapped on the drawing are drawn out separately at the left); center right, plant from Fourche a du Clos, Mo., drawn at two levels with nucleolus repeated as a reference point; center left, plant from Dederick, Mo.; lower right, plant from seed collected at Rogers, Ark.; lower left, plant from Spencer Co., Ind.

quite evident that there is a good deal of variation in size between bivalents.

In the plants with a 2n number of 72, multivalent configurations were found in every cell. Both in the material from Virginia and that from southern Indiana, cells with 30 configurations were very common. Unfortunately, the size range of bivalents is so great and the contraction can be so extreme that it is not always possible to distinguish between a small bivalent and a large univalent. Nothing was seen which, by comparison with the diploids, was certainly a univalent although there was an occasional configuration which might possibly have been one. In those multivalents whose structure could be made out with certainty only quadrivalents were recognized. These were all open rings of 4 or open chains of 4. Closed figures of 8, closed rings of 4 (all 4 united at each end) cross-shaped quadrivalents, and rings of 2 united to chains of 2 were not seen, though in such highly contracted chromosomes some of these configurations would have been difficult to make out if they had actually been present. Disjunction of the multivalents seemed to be regular at metaphase, and no micronuclei or other irregularities were noted in young microspores.

Discussion.—Eighteen is the lowest number of chromosome pairs yet reported for any *Tripsacum* (Reeves and Mangelsdorf[6]; Longley[7]), but in the closely related genus *Manisuris* there is one species with 9 pairs of chromosomes[6]. This suggests that Tripsacums with 18 pairs of chromosomes may themselves be tetraploid. Since polyploidy of a high order is very frequent in the Gramineae this does not appear at all unlikely. Furthermore, the complex morphological relationships between *Manisuris*, *Rottboellia*, *Tripsacum*, etc., suggest that they may all be part of an intricate polyploid complex. *Manisuris cylindrica*, for instance, was originally regarded as a species of *Tripsacum*, to which genus it shows a very strong natural resemblance. However, it has perfect flowers, a character which technically would remove it completely from the tribe Maydeae. By various experts it has been assigned to the genus *Rottboellia*, to *Coelorachis*, and to *Manisuris*, nor is it the only species in this group of genera whose position has been generally uncertain. The fact that *Manisuris cylindrica* is almost identical with *Tripsacum*, aside from its perfect flowers and that it has half the chromosome number of the lowest reported *Tripsacum*, would suggest that the 18-paired Tripsacums are themselves tetraploid. However, since they show little or no multivalent association, they are most probably amphidiploid derivatives of distantly related diploids. The cytological evidence would suggest that the 18-paired Tripsacums might have a cytological formula of XXYY where X and Y stand for sets of 9 chromosomes, and that *Manisuris* might be XX on the same notation. The taxonomic confusion in this group of genera is exactly what would have resulted had such inter-generic (and probably inter-tribal) reticulate relationships become established.

[6] Reeves, R. G., and P. C. Mangelsdorf. Chromosome numbers in relatives of *Zea Mays* L. Am. Nat. *69*:633-635. 1936.
[7] *loc. cit.*

The chiasma frequencies and multivalent frequencies noted above can be used to suggest the possible relationships between the 18- and 36-paired Tripsacums. With a frequency of approximately 2 per bivalent (such as that reported above) and on the simplest possible assumptions we would expect an auto-tetraploid to form quadrivalents two-thirds of the time and pairs of bivalents one-third. (With 2 chiasmata per bivalent we expect one at each end. If among the homologous chromosomes 1, 2, 3, and 4, chromosome No. 1 pairs with No. 2, then at its other end it is equally likely that it pair with 2, 3, or 4. Pairing with 3 or 4 will produce quadrivalents, with 2 will produce 2 bivalents.) If the 36 Tripsacums are auto-polyploids we would expect two-thirds of them to produce quadrivalents and one-third bivalents. This would result in 12 quadrivalents and 12 bivalents, a total of 24 configurations per cell. If, however, they are amphipolyploids between related tetraploids (some such relationship as that between XXYY and XXZZ) then we would expect 30 configurations, the number actually observed. (Using XXYY and XXZZ to diagram the putative parental Tripsacums then we would expect the 9 sets of X's to form 6 quadrivalents and 6 bivalents, the Y's to form 9 bivalents and the Z's to form 9 bivalents, a total of 30 configurations).

The above computations should not be taken too seriously since they probably represent an over-simplification of what occurs and since the chiasma frequencies are based on estimates. However, they are put forward with more confidence since the observations preceded the computations. The estimate of 30 configurations was made so repeatedly in different smears of the 36-chromosomed plants from Indiana that a search was made through the records to find what has been noted about the Virginia plant when it was studied two years before. When the notes showed that it too had an overwhelming number of counts of 30, the computations were undertaken to see on what conditions such a number could be obtained. Since the Virginia and Indiana plants show certain constant morphological differences from the 18-paired plants of the prairies and Great Plains the simplest hypothesis was to assume that if the 18's were tetraploids of the constitution XXYY then the 36's were octoploids of the constitutionXXYYXXZZ. The fact that the computations agreed exactly with the observations is more likely a happy coincidence than it is an exact scientific verification. It does, however, seem fairly certain that the 36's are not autopolyploids and that they must have roughly some such formula as the one suggested.

SUMMARY

1. The difficulties of maintaining a collection of *Tripsacum* plants are described.

2. Chromosome counts are reported for *Tripsacum dactyloides* collected at various points throughout its range. In the prairies and Great Plains this species has 18 pairs of chromosomes. Along the eastern seaboard it has 36 and in Texas both numbers have been reported.

3. The 18-paired plants undergo regular meiosis with no multivalent associations. Those with 72 chromosomes averaged 6 quadrivalents and 24 bivalents. Chiasma frequency in the former is at least 2 per bivalent.

4. On the basis of these observations and the general morphology of *T. dactyloides*, it is suggested that the 18-paired varieties of *Tripsacum* may be amphidiploids of the formula XXYY and that the 36-paired varieties arose as octoploids (XXYYXXZZ) between XXYY and XXZZ varieties.

HOMOLOGIES OF THE EAR AND TASSEL IN *ZEA MAYS*

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The exact correspondence between the variation of the male and female inflorescence of *Zea Mays* is a problem which has attracted a number of minds and has produced several theories, none of which completely satisfied the existing data. The morphological facts have been assembled by Weatherwax ('23, '35), and he, Collins ('19) and Kempton ('19) have reviewed the pertinent literature. After surveying all the existing evidence Collins' final conclusion was that, though he had used the hypothesis of a shortened and twisted central spike to explain the results in crosses between *Zea* and *Euchlaena*, "facts of other kinds are more easily interpreted by the theories of fasciation and reduction of branches . . . . There are also facts that do not seem to accord with any of the theories yet proposed. Until the apparently contradictory evidence can be reconciled, it seems best to keep the several possibilities in mind and await additional evidence before attempting a complete interpretation." Though the facts reported below shed further light on the problem, Collins' words of caution are still in order and the complete solution, while perhaps not far distant, is still to be awaited. Though he disagreed rather completely with Collins on other points, Weatherwax's final conclusions ('23) concerning the ear were very similar. "The last word has not yet been said on the evolution of the ear of corn, and it cannot be said until further researches have corrected, amplified, and evaluated the data now at hand, and woven the results into a harmonious theory." [loc. cit. pp. 112-113].

Earlier workers were interested in the problem of ear and tassel relationships chiefly from theoretical considerations. With the development of large-scale scientific maize breeding in the U. S. cornbelt, it is now a problem of considerable economic importance as well. If a corn breeder could size up the potentialities of the ear, merely by examining the tassel, he could take many short cuts, both in the creation of new inbred lines and in maintaining their desirable characters.

Methods.—The general method of work is discussed in some detail since in the author's opinion it is of even greater significance than the results themselves (though, as will be demonstrated below, useful correlations have already been established by these methods). In beginning the work, a few tassels were examined in great detail, with particular reference to the structures considered significant by systematists: glumes, spikelets, pedicels, secondary and tertiary branches, etc. With these facts thoroughly in mind, as many kinds of maize as possible were grown and examined. A particular effort was made to secure rare and unusual varieties, especially those from Central America and South America.

The work was begun in 1941. By 1944 the general pattern of variation in tassel morphology was apparent. Then, for the first time, a serious effort was made to compare tassel and ear morphology in segregating families and in inbred lines of maize. A preliminary study of various inbreds from the U. S. Department of Agriculture and several agricultural experiment stations had indicated that this might be a fruitful method of investigation. Among the old well-established inbred lines used in modern hybrid corn breeding, there are many with extreme tassel types and ear types. Furthermore, they are practically pure breeding and they can be compared when planted in different soils, at different times of year and in different places. Through the kindness of the Pioneer Hi-Bred Corn Company, the inbred plots and breeding records of this company were put at my disposal in the summer of 1944. By a fortunate circumstance their breeding farm is not far distant from the Iowa Agricultural Experiment Station at Ames, where a further set of highly significant inbreds and hybrids was obtained from Professors E. W. Lindstrom and J. C. Eldredge. I am very much indebted to these individuals and institutions who have allowed me to study tassel morphology in their own experiments, most particularly to Mr. Raymond Baker of the Pioneer Hi-Bred Corn Company. His encouragement and cooperation have made possible this preliminary report though he is in no way responsible for its shortcomings.

The general method of work was to select either F_2 segregates or a series of inbreds with some outstanding characteristic of the tassel and then to examine the ears for possible correlations. When one was suspected, more material was examined to see if the correlation still held. The customary procedure in such cases was to walk rapidly through the breeding plots, keeping an eye out for tassels which were very extreme for the character under observation, and then to study the ears on these plants. When an ear-tassel correlation was at length apprehended, various methods of recording it were tried out. It was then measured precisely in a series of inbred lines, and the figures so obtained were compared not only with the actual ears borne by these inbreds but also with their progeny in controlled crosses. For instance, it was suspected that the length of the upper tassel branches was an important factor in ear length; Lindstrom's LA inbred line of maize was found to be an outstanding inbred line in the length of its upper tassel branches. Not only did it prove to have a long ear for an inbred; a reference to breeding records showed that on the average it had transmitted longer ears to its progeny than any of the other inbreds with which it was being compared. To summarize: tassel variation was studied in a general way for three years before precise correlations of ear and tassel were attempted. Even then, they were first run to earth by quick qualitative methods before they were submitted to statistical treatment.

It is unfortunate that much of the so-called quantitative investigation in this country is done in exactly the opposite fashion. In many laboratories measurements are taken by the hundred and are then submitted to mathematical analysis

in the hopes that useful results will emerge. This is putting the cart before the horse. It is a fundamental principle, too often ignored, that before a biological phenomenon is to be investigated on the mathematical level it must first be thoroughly analyzed on the biological level. One must first understand in at least a general sort of way what is happening in the material under investigation before he can set up an efficient measure of that particular phenomenon. The ear-tassel correlation problem is an instructive example. In terms of what one human being can accomplish in a life time, the numbers of features of maize ears and tassels which might be measured are almost infinite. It is scarcely to be wondered, therefore, that few significant results were obtained by those who studied ear-tassel correlation with an electric computing machine (Collins, '16; Kempton, '26). Statistical analysis has a useful place in biology but it must be preceded by biological analysis.

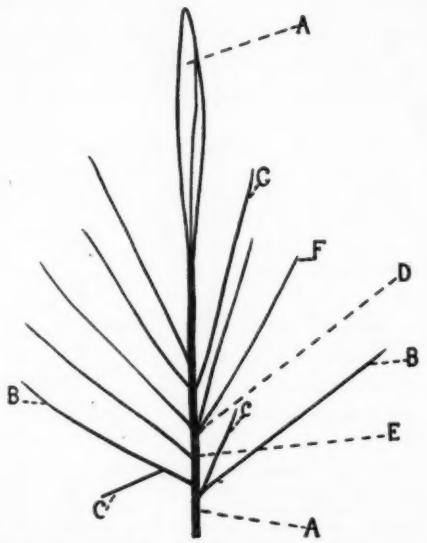

Fig. 1. Diagram showing main features of male inflorescence ("tassel") of *Zea Mays*. Further explanation in text.

Tassel Morphology in Zea Mays.—In order to grasp the following discussion it will be necessary to have the fundamental ground-plan of the male inflorescence of maize (the tassel in common speech) thoroughly in mind. Its branching system is illustrated diagramatically in fig. 1; certain variations in the arrangements of the spikelets are shown in fig. 2. The tassel always consists of a primary axis (AA), fig. 1, usually with a certain number of secondary branches (B, F, G, etc.). The lower secondaries may themselves branch at the base giving rise to

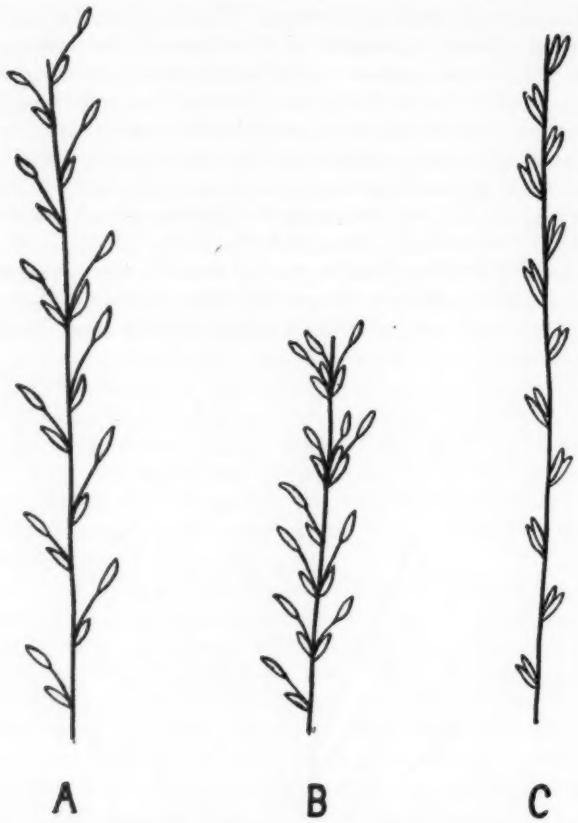

Fig. 2. Diagram showing variation in spikelet arrangement on secondary tassel branches in North American strains of *Zea Mays*. 'A' shows very slight condensation of internodes; 'B' shows higher condensation; 'C', the extreme of a common North American tendency, the shortening of the pedicel in the pedicellate spikelet. Further explanation in text.

tertiary branches (C). The primary axis is terminated by the central spike (A). The secondaries may all arise separately from the primary axis or a part of them may be whorled (D) or, in rare cases, they may all be in whorls of 2 or 3. The number of secondaries varies widely even under the same cultural conditions and is usually quite constant in inbred lines. There are occasionally only 1 or 2 (in rare cases none), or there may be up to 40 or more in each tassel. The length of the secondaries varies greatly as well as their comparative lengths along the tassel.

Figure 2 diagrams the manner in which the spikelets are arranged upon the branches of the inflorescence. The maize of the American corn belt is highly

variable for this character, as will be discussed below. 'A', in fig. 2, diagrams the simplest arrangement and one which is, from a technical agrostological point of view, the normal one for *Zea Mays*. The spikelets are arranged in pairs, one spikelet in each pair being sessile and one pedicellate. In North American maize there is great variation in the length of the pedicel and in some inbred lines the condition may be like that illustrated at 'C' where the spikelets are in pairs but the members of each pair are practically indistinguishable in pedicel length.

All North American dent corn has a considerable number of condensed or telescoped internodes as illustrated in 'B'. Sometimes the condition is no more extreme than illustrated at 'A'. The fifth node from the apex is really two nodes and bears two pairs of spikelets instead of one. The example shown at 'B' is by no means extreme, and there are many inbred lines and Mexican varieties which show twice as much condensation as this. The tassel branch segment in 'B' has exactly as many spikelet pairs as 'A' and 'C' but many of the internodes are condensed. From the apex to the base the number of spikelet pairs at each apparently single node are 3, 3, 1, 2, 2, and 1. Technically, of course, there are 3 fused nodes at the first, each with its own pairs of spikelets, 3 at the second, and so on down the stalk.

Inbred lines of maize vary in the angle at which the secondaries leave the primary axis and the angle is usually surprisingly constant for each inbred line. In certain inbreds it is sometimes constantly under 10 degrees; in other inbreds it may even exceed a right angle.

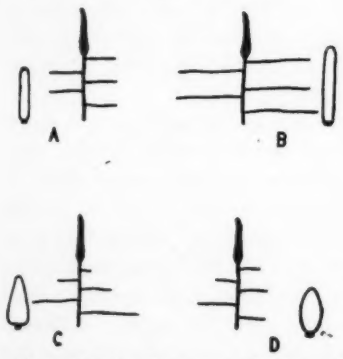

Fig. 3. Relation between tassel shape and ear shape in *Zea Mays*; highly diagrammatic. Further explanation in text.

Maize from different parts of the New World, as well as inbred lines, varies greatly in the position at which the lowest spikelet pair is set on the secondary. In some Mexican varieties and certain commercial inbreds it is so close to the base of the secondary that it almost seems to arise from the primary axis. In most high-altitude South American varieties, the secondary has a long basal internode below the first spikelet pair. In our notes, this is referred to as the "sterile zone" and is usually measured on the third secondary from the base of the tassel.

Correlations.—It may make the discussion easier if we anticipate the general conclusions from the data before presenting the results in detail. The correlations between tassel and ear are those which would result *if* the ear *were* composed of branches fused spirally about a central cylinder (see fig. 3). The actual correlations are a fact. Their interpretation is quite another matter and is discussed

briefly on page 338. Figure 3 demonstrates, for several extreme tassel types, the fairly precise correspondence between the "profile" of the tassel branches and the shape and size of the ear. However, all of these patterns are affected by the degree of condensation which varies independently of the number of tassel branches and their absolute and relative lengths. It will, therefore, be necessary, first of all, to discuss ear-tassel correlations for condensed internodes.

Condensation.—As has previously been explained, the internodes of North American maize tassels may frequently be condensed or telescoped. Sometimes an internode is extremely shortened but is still visible as a separate internode. More frequently 2, 3 or even 4 internodes are so foreshortened that they give the appearance of a single node bearing 2, 3, or 4 pairs of spikelets. It is, in other words, a kind of controlled fasciation which operates throughout the plant. In the ear, it is one of the factors controlling row number. As will be demonstrated below, there is in North American maize a surprisingly close correlation between the condensation of the tassel and the degree to which row number is increased above 8 or 10 rows. For several reasons, condensation can be studied much more effectively in the tassel. In the first place, the tassel is apparently much more sensitive, and a low degree of condensation which will not reach a threshold of expression as to row number can be exactly measured there. In the second place, the ear is a highly complex organ in which it is difficult to detect the individual effects of various developmental factors. The tassel is much more simple and in it the effects of condensation can be studied independently of other factors. In the tassel, for instance, one may study condensation, the development of secondary and tertiary branches, and whorled branches vs. alternate or spiral branching, and all three can be followed as independent variables. In the ear they all affect row number in one way or another.

The genetic background of condensation is obscure. It seems to be a kind of fasciation due either to a single mutant gene and a large number of minus modifiers or to a large number of genes which produce the same general effect. It has a pronounced geographical distribution which is exactly that of denting. Though dented kernels and condensation are different things genetically they are both found in an exaggerated degree in the Mexico City-Toluca neighborhood (Anderson, unpublished) and seem to radiate from there in all directions. From archeological evidence we know they have been there for at least a thousand years and that it is apparently the center to which all our North American dent corns can be traced back.

The number of spikelet pairs per internode (and therefore the degree of condensation) varies within very wide limits, and these extreme types are characteristic of two widely separated areas in the New World. The varieties of high altitudes in South America have little or no condensation in the secondaries. A specimen tassel grown in the United States from Peruvian seed had the following number of spikelet pairs per node on its lowest secondary branch (scored from

base to the tip, node by node): 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 2, 1, 1, 1, 1, 1, 1, 1, 1. The opposite extreme is found in the dent and pop corns with sharply tapering ears ("Mexican Pyramidal" of Anderson and Cutler, '42) which are the typical maize of the region around Mexico City. Popcorns similar, if not identical, are grown in the United States under the name of "Japanese Hull-less" (a misleading name since they are apparently no more Japanese than they are hull-less). The lowest secondary branch from one of these pop corns scored as follows: 1, 1, 1, 1, 1, 1, 1, 1, 1, 2, 2, 2, 4, 4, 4, 4, 5, 3, 3, 4, 4, 4, 3, 3, 3, 1, 1, 1. In order to facilitate exact quantitative comparisons between tassel condensation and ear row number, these raw data need to be converted into a single score. This is a little difficult since sometimes the basal portion of the tassel will be most condensed, sometimes the entire tassel, and sometimes merely the terminal portion. Average condensation per node is not too significant since few tassels are highly condensed for their whole length and the great majority have at least a basal or terminal portion which is quite uncondensed. After comparing a great variety of condensation patterns the following procedure was worked out and gives a fair and objective index for making exact comparisons. The apparent number of nodes is counted and the central three-quarters are selected for computation. If there are 36 nodes, for instance, the central 27 are used. The quarter which are discarded are the least condensed nodes at the base, or at the tip, or both. However, they are consecutive nodes at each of these points. If the tassel in question had had no condensation for 10 or so nodes at its base, then all the discarded nodes would have been basal; if it had had such an area at the apex, then all the discarded nodes would have been from that area; if it had had four uncondensed nodes at the base then the basal 4 would have been eliminated from the computations as well as 5 from the tip to make up the 9 nodes. For the central three-quarters of the tassel, the total number of spikelet pairs in that portion is divided by the number of nodes. This gives an index running from 1.0 to 4.0, or even a little higher. This condensation index can be defined precisely as "the average number of spikelet pairs per apparent node in the most condensed central three-quarters of the basal-most secondary branch of the male inflorescence." All of which sounds very much more complicated than it actually is. In common speech it could be rendered as, "a precise measure of how thickly the male flowers are set together in the lower part of a corn tassel." Most of the South American maize which has been examined scores 1.0 on the Condensation Index and the maize of western Mexico is 1.0 to 1.4. Maize of the Mexico City-Toluca area scored from 1.5 to 4.2. In the U. S. corn belt one open-pollinated field of Reid's Yellow Dent scored from 1.0 to 2.2. Forty of the commoner inbreds used in hybrid corn breeding had indices from 1.0 to 3.0, the average (median) being at 1.6.

For North American maize the Condensation index, as calculated above, proves to be a fairly precise measure, not only of tassel condensation, but of potential ear row numbers. We may anticipate the evidence given below and state that for

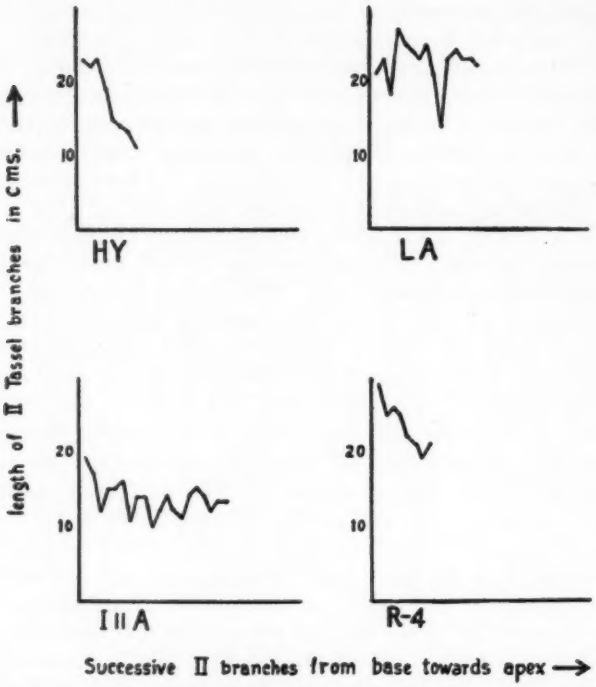

Fig. 4. Tassel branch profiles of four inbred strains of *Zea Mays*. The lengths of successive secondary branches are plotted, one after the other, and joined by a line. Further explanation in text.

much of the corn of the U. S. corn belt, the ear row number is equal to roughly ten times the condensation index, or in mathematical notation:

$$\text{Row number} = 10\ \text{CI}.$$

As has been suggested above, row number and row pattern are affected by various factors but in much of the maize of the United States, condensation is the chief variable. For all practical purposes we can assume that North American maize has a "fundamental" row number of 8 or 10 and that any increase above this number will be directly proportional to the Condensation Index as calculated from the tassel. This is not just a theory; it has been experimentally verified in a wide variety of inbred, hybrid, and open-pollinated material. Before discussing it, it will be necessary to review the evidence for variability in row number. This character, as might be expected, is influenced not only by inherent capacity for many or few rows, but by the vigor of the plant and by environmental influences. Even highly homozygous inbreds and first-generation hybrids may vary considerably in row number. The latter, as is well known, is always an even number since the fundamental variable is the number of alicoles, each one of which gives

rise to two rows (Collins, '16). A hybrid which is characterized by 14 rows may bear a good many ears with 12 and with 16 rows. A weak inbred which averages only 14 ears may behave in crosses as though it averaged 16, etc.

One of the most precise tests for the exact correspondence between row number and the Condensation Index was afforded by Lindstrom's PR inbred and its remarkable mutant PR-M. As Lindstrom has stated ('40), the former is potentially 20-rowed and the mutant is potentially 16-rowed. Fifteen tassels of each were examined. The average Condensation Index for the PR tassels was 2.2; for the PR-M tassels 1.7. If we assume that the row number divided by the Condensation Index will give us what the rowing would have been without condensation, we may divide 20 by 2.2 for PR and 16 by 1.7 for PR-M. The answer to the nearest round number is 10 for each. In other words, the higher degree of condensation in the tassel of PR as compared to PR-M is exactly proportional to the increase in ear row number.

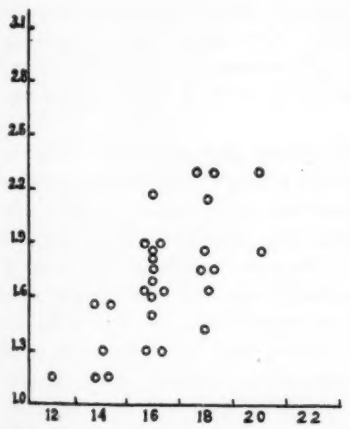

Fig. 5. Scatter diagram showing the correlation between tassel-node condensation and ear row number in a group of F_1 crosses between inbred lines of commercial corn. Vertical scale, *average* condensation index of the two parental inbred tassels. Horizontal scale, number of rows of kernels on the ears of the F_1 hybrid plants.

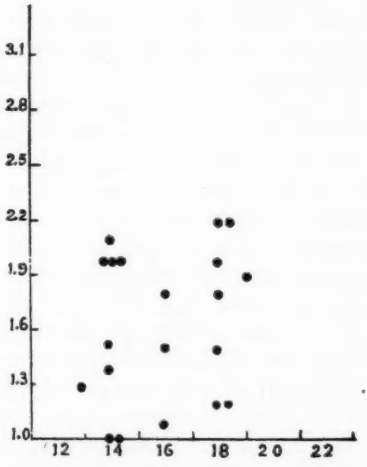

Fig. 6. Scatter diagram showing correlation between tassel-node condensation and ear row number among 21 plants of a back-cross between two inbred lines of yellow dent corn. Each dot represents a single plant. Vertical scale, condensation index of the tassel; horizontal scale, number of rows of kernels on the ear.

Another precise test was afforded by a series of standard commercial inbred lines of maize and their F_1 hybrids, selected from breeding plots of the Pioneer Hi-Bred Corn Company. The inbreds were being grown in short rows for observation. After a quick inspection, a single representative tassel was chosen from each inbred, and the Condensation Index was calculated in the manner described above. The average Condensation Index for any two inbreds was then calculated

and compared with the actual row number obtained in a hybrid between these two inbred lines. Here again, only one plant was examined. No conscious selection was made other than to see that the ear was obtained from a healthy plant with no obvious malformations. The correlation between tassel condensation and ear row number is presented in fig. 5. Considering the variability of row number this is a remarkably high correlation, especially when one considers that neither tassel condensation nor ear row number was an average value, but was merely a single selected individual. It will be noted that for lower values of the Condensation Index the row numbers are on the average about 10 times the Index but that for higher values these potentialities are not realized. It may be that, under the conditions of the experiment (the plants were being grown three to a hill), the plants with high condensation were not able to reach their full potentialities. It is also possible that in corn-belt maize there has been a strong selection of modifying factors which would keep the high degrees of condensation under control. It is certainly true in Japanese Hull-less popcorn, where these "bearpaw" ears have not been selected against, that highly condensed tassels are accompanied by equally highly condensed ears. One tassel selected because it was highly condensed along its whole length, with an average condensation of 3.3, had 32 rows of kernels; a much less condensed tassel, with an Index of Condensation of 2.1, had 24 rows of kernels.

Figure 6 shows the same kind of scatter diagram in a population where the effects of environment are much more severe and a less close correlation would be expected. A hybrid between two inbred lines was back-crossed to one of the parents, and these were planted three to a hill in a large plot. In the previous example, while the hybrids were subject to this same crowding, they were all planted with individuals of their own genetic constitution, and interaction between plants was relatively constant throughout the experiment. In this back-cross the plants varied in their general vigor. A strong plant which happened to be in the same hill with two quite weak siblings had an excellent opportunity to reach its full potentialities; a weak plant in the same hill with two very strong ones could not have been expected to do so.

Finally, fig. 7 diagrams a larger population in which the interaction between the three plants in each hill is somewhat less extreme. In this case ear-to-row tests were being made of an open-pollinated strain of a long-eared yellow dent. One healthy, vigorous plant was selected in each row and its row number and Condensation Index were obtained.

There is even a correspondence between the condensation *pattern* of the basal-most secondary branch of the tassel and the flattening of the ear. If the tassel branch is highly condensed along its entire length, then the ear will be a true "bearpaw." If the tassel branch is highly condensed at the tip but much less so below, then the ear will be more or less circular in cross-section with a flaring, usually two-pointed apex. If the tassel branch is highly condensed at the base but runs out into a long uncondensed portion, then the ear will be broadly

elliptic at the base but with a normal apex. No exceptions to this generalization have been noted in all the material which has been examined. Plate 17 shows three very different ears of maize with very different degrees of condensation and different condensation pattern. In all three, if the actual row number is divided by the Condensation Index calculated for the tassel, 10 is indicated as the "fundamental" row number.

The pattern of condensation in the lowest tassel branches of the three ears is as follows (in each case the figures indicate the number of pairs of spikelets at each apparent node, beginning from the base):

Mexican "Bearpaw" dent—2, 3, 3, 2, 2, 2, 4, 4, 5, 3, 4, 3, 3, 3; 3, 4, 2, 4, 2, 3, 3, 3, 3, 2, 1, 3, 3, 3, 3, 5, 4, 3, 4, 4, 3, 3, 4, 2, 3, 3, 3, 4, 2, 2, 4, 3, 4, 4, 3, 2, 3, 2, 4, 3, 2.

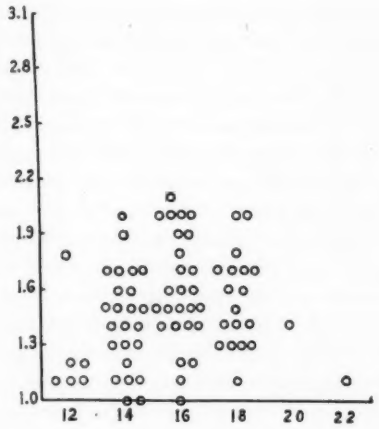

Fig. 7. Correlation between condensation of the tassel and row number of the ear in an ear-to-row plot of long-eared yellow dent. Scales as in figs. 5 and 6. Further explanation on p. 334.

Open-pollinated long-ear Reid—1, 1, 1, 1, 1, 2, 2, 2, 1, 2, 2, 2, 1, 3, 3, 1, 1, 2, 3, 3, 3, 4, 3, 5, 4, 5, 4, 5, 4, 5, 4, 4, 4, 1; 3, 1, 3; 2; 3, 1, 2; 2.

Inbred Os 420—1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 2, 3, 1, 1, 2, 1, 1, 1, 1, 1, 2, 1, 1, 2, 1, 1, 1.

There is a close correspondence between these patterns and the ears. The tassel of the "Bearpaw" dent is highly condensed along its whole length; so is the ear. The tassel of the open-pollinated yellow dent is slightly condensed below but very heavily condensed towards the apex; the ear has 18 rows at the base but is fasciated at the apex with approximately 22 rows. OS 420 has only a light degree of condensation throughout its tassel and it has an ear with 14 rows.

Tassel profile and ear shape.—As shown schematically in fig. 3, there is a surprisingly close correspondence between tassel branch length and ear length and between the relative lengths of successive tassel branches and the shape of the ear. If the tassel branches are all long, as in fig. 3, 'B', then the ear is long and cylindrical; if they are all short (fig. 3, 'A'), then the ear is short but still cylindrical. If the branches get successively shorter towards the apex, then the ear tapers sharply and regularly (fig. 3, 'C'). If they are short both at the base and the apex and longest in between (fig. 3, 'D'), then the ears have a kind of "hand grenade" shape as in certain sorts from South America.

This correlation is more than a general one between different races of maize; if used in conjunction with the other correlations reported in this paper it may even be used to judge between related inbreds. It apparently is highly correlated not only with the actual shape of the inbred ear but also with the behavior of the inbred in crosses. Tassel branch diagrams are presented in fig. 4, using a modification of the simple method recently described by Anderson and Schregardus ('44). It will be seen that the "profile" of the tassel established in fig. 4 is an excellent reflection of the known behavior of these inbreds. Inbred LA is known to produce long cylindrical ears in single crosses with other inbreds while inbred HY is also notorious as producing sharply tapering ears in crosses with other inbreds. Preliminary indications are that the tassel profile may even be a better indication of ear-shape potency than the actual ear of the inbred itself. Some 40 inbreds were carefully examined and their tassel profiles were compared with the ears. All agreed in a general sort of way though there were a few exceptions. These exceptional profiles agreed better with the breeding records than the ears themselves. Figure 4 shows a case in point, the profiles of inbreds Ill. A and R-4. The profile of the former suggests a short, nearly cylindrical ear. The profile of R-4 suggests a long ear, tapering pretty sharply, though not as extreme as HY. The actual ears of these inbreds are somewhat as indicated, but when compared with each other they are very much alike; much more so than the tassel profiles. However, both of these inbreds are widely used commercially. It is well known that in hybrids, R-4 produces a much longer but more tapered ear than does Ill. A.

In the material which has been investigated there is even some indication that if the first one or two tassel branches are markedly longer than the rest there will be a tendency for the basal portion of the ear to be somewhat larger. This correlation rests on scattered observations and needs to be carefully tested with lines which are reasonably constant for other characters but differ in the basal enlargement of the ear or the length of the lowest one or two tassel branches.

Tertiary tassel branches and irregular rowing.—The kernels of an ear of maize may be spaced either evenly or unevenly. A little examination will show that the unevenness is due to two quite different factors. The rows may be regular but the kernels set crookedly in the row, or the rows themselves may be irregular

in spite of the fact that the kernels are set straight in the rows. This latter condition is, among other things, correlated with the number of tertiary branches on the lower secondary branches of the tassel. Here again, the two extreme conditions have marked geographical distributions. The common dent varieties of the American corn belt have an intermediate condition between these two extremes, and ordinarily have 1 or 2 of the lower secondaries which bear tertiary branches, usually not more than 1 or 2 tertiaries arising from each. In the Peruvian area 6 or more of the basal secondaries may bear tertiaries. There are frequently 5 tertiaries on the basal-most secondary, and the larger tertiaries may themselves give rise to short branches of the fourth order. Similar tassels are also to be found in Guatemala. The other extreme is found most highly developed in Mexico where in spite of the fact that the tassels are often very large, tertiary branches are few or none.

If the ear were formed *as if* the tassels were wrapped spirally about a central core, then one might expect these short tertiary branches to upset the rowing. Such is probably the case. As with the factor for condensation, there is apparently a lower threshold for expression in the tassel than on the cob. A tassel with one or two tertiaries is not always accompanied by irregular rowing. However, inbred lines characterized by highly irregular rows have a high degree of tertiary branching in the tassel. There even seems to be a rough correspondence between the comparative length of the tertiaries and the place on the ear where the irregularities appear. These may take two forms. Ordinarily, they show as a place where the row runs out. Sometimes, however, they merely appear as an extra grain inserted between two adjacent rows.

Further correlations are suspected but will require detailed examination of critical material to establish. These are as follows: (1) a positive correlation between the size of the primary axis at the base and the size of the shank and cob, (2) a positive correlation between the number of tassel branches and the comparative size of the pith zone in the center of the cob, (3) a negative correlation between the angle made by the primary axis and the secondary branches of the tassel and the brittle-stiffness[1] of the main stalk of the corn plant, (4) a correlation between very large, rough, pointed spikelets and long, more-or-less pointed kernels.

Discussion.—The correlations outlined above are definite enough to be of some use in practical maize breeding. This does not necessarily mean that they are decisive evidence in the old controversy as to whether the ear of corn is homologous with the central spike of the tassel or whether it is homologous with an entire tassel of fused branches. When we come to understand the tassel and the ear not merely as end products but in terms of the actual forces which mould them as they are, we may find that both of these concepts have their place. It is quite possible that, in so far as some forces are concerned, an entire ear is like the central

[1] No one English word expresses this quality.

spike of the tassel, but that in terms of other forces it is more exactly homologous with tassel branches fused spirally side by side. An extension of the general method described in the introduction should make it possible to settle such questions fairly definitely.

The observations reported above do provide fairly clear evidence with regard to the old controversy as to whether or not the ear of maize is fasciated. The "condensation" reported above is a kind of regular, controlled fasciation which only occasionally becomes so extreme as to produce elliptical axes and multiple growing-points. The new evidence also suggests quite as clearly that fasciation is only one of several forces and that in North American maize it operates only in ears of more than 8 or 10 rows. The whole history of the maize ear is much too complex to discuss here even in a preliminary fashion. Understanding that the condensation of North American maize is a special feature and that it apparently traces back to the Mexico City-Toluca area and is tied up with the history of dents and "bearpaw" popcorns should enable us to approach the larger problem more intelligently. Apparently, primitive South American maize had a whorled tassel and a short, ovate or top-shaped ear with regularly disposed kernels but no straight rows, as we know them in modern maize. Some unexplained agent, perhaps *Tripsacum* (Mangelsdorf and Reeves, '39), introduced long straight rowing and alternate or spiral tassel branches. The extremely simple 8-rowed flints are not among the older prehistoric remains either in South America or in the American Southwest. The straight 8-rowed ear is apparently a highly derived rather than a primitive condition in *Zea Mays* (if we consider that remarkable aggregation of forms *as a whole* and not merely from the point of view of the American corn belt). Increase in row number in South American varieties is accompanied by an increase of condensation in the central spike but apparently not in the tassel branches. This is one of many points concerning condensation that needs further investigation.

Little has been said concerning the genetics of any of the characters described above. They are all apparently multiple-factorial. Preliminary evidence suggests that the factors are not scattered at random through the chromosomes. An extension of the methods of analysis outlined above should make it possible to begin the exact genetic study of quantitative characters in maize. Emerson and his co-workers have already assembled a series of marker genes and an effective cooperation between different laboratories. Unfortunately, however, the chief character (ear row number) which has so far been investigated (Emerson, '32) is one which does not lend itself well to exact analysis. Since the difference between an easily recorded character and an easily analyzed character does not seem to be generally understood it may be well to amplify this *dictum*.

Ear row number is a good example of a quantitative character which is easy to record exactly but difficult to analyze. Any ordinary ear of maize has just so many rows and there is no quibble about it. However, we are not interested as geneticists in the number of rows; we want to find out something about the

forces which go to make low row number or high row number. As has been demonstrated above, these forces are of various kinds, *each one a quantitative multiple factor character in itself*. Before we can analyze the genetics of row number we must, first of all, break it down into its component forces. The section on "Condensation" presents data which suggest that condensation is *one* of these components. With the method of tassel scoring outlined above, it should be possible to study the genetics of this primary multiple factor character and learn where the genes for condensation are and how many there are and how they interact. The other factors affecting row number will then be easier to analyze, but serious genetic analysis must again be preceded by morphological detective work.

Just as the early work on the genetics of eye-color mutants and wing mutants in *Drosophila* was based upon long hours of study and scrutiny by such gifted observers as the late Calvin Bridges, so any serious attempt to study the genetics of quantitative characters must be preceded by explorative observation. It is generally admitted that the genetics of quantitative characters is much more difficult than that of single factor mutations. After a decade of work, I am convinced that the preliminary observational analysis of quantitative characters presents unsuspected difficulties; difficulties, furthermore, of a higher order of complexity. It is indeed a research field in its own right. Although plant material is apparently easier to analyze morphologically than either vertebrate or insect material, it will require long and coöperative preliminary research if problems concerning quantitative characters are to be brought to the level where they are ready for genetic analysis. A series of apparently unrelated papers which have emanated from this laboratory in the past decade (Anderson and de Winton, '35; Anderson, '39; Anderson and Ownbey, '39; Anderson and Hubricht, '43; Anderson, '44; and Anderson and Schregardus, '44) are all connected in one way or another with this problem. While some of them have so little apparent connection with plant genetics that they could not have been published in a journal devoted to that subject, they are all concerned with multiple factor genetics. They represent various attempts to work out methods for analyzing quantitative characters on a morphological level. In this paper I have attempted to demonstrate how such techniques might be applied to practical maize-breeding problems.

SUMMARY

1. The methods used in this study are described. The necessity of analyzing the material on a biological level before statistical methods are applied is stressed and illustrated by examples.

2. Variation in the tassel (the male inflorescence of *Zea Mays*) is described, character by character, and methods of recording it exactly are outlined.

3. Evidence for the following ear-tassel correlations is presented:
   a. Tassel internode condensation and increase in row number.
   b. Tassel branch length and ear length.

c. Tassel branch pattern and ear shape.

d. Tertiary branches and irregular rowing.

4. In North American corn, the relation between tassel condensation and row number is surprisingly exact. In general, it is close to the following equation:

Condensation Index = row number /10.

5. The geographical distribution of tassel condensation is discussed. It reaches its highest development in the Mexico City-Toluca area which is also the center for extreme denting.

6. The problem of homologies between tassel and ear is briefly discussed. It is tentatively concluded that in so far as the actual forces are concerned *both* the fused tassel branch hypothesis and the central spike hypothesis may be essentially true.

7. The application of these facts to the genetics of quantitative characters is discussed briefly. Using condensation as an example, a distinction is made between multiple factor characters which can be recorded exactly and those which can be analyzed exactly.

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Explanation of Plate

PLATE 17

Three ears which illustrate the correspondence between the condensation of nodes in the tassel and the increase in row number of the ear: Left, inbred yellow dent Os 420; center, "bearpaw" dent from Mexico; right, open-pollinated yellow dent from Iowa. (N. B. This ear *is* right side up; the feature at the apex is the expanded tip of the cob.)

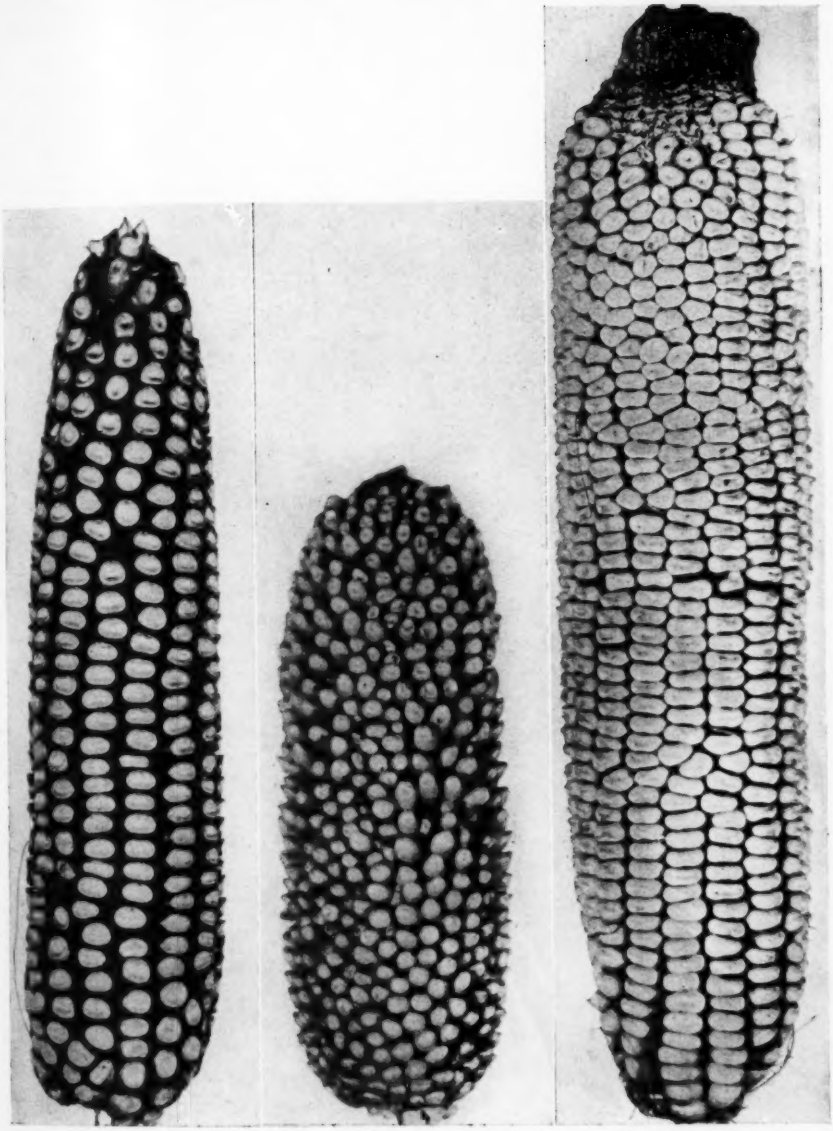
Condensation indices and condensation patterns for these ears are as follows, the figures representing the number of spikelet pairs per node beginning at the base of the lowermost tassel branch:

Inbred Os 420
C. I. = 1.4
1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 2, 3, 1, 1, 2, 1, 1, 1, 1, 1, 2, 1, 1, 2, 1, 1, 1

"Bearpaw" dent
C. I. = 3.2
2, 3, 3, 2, 2, 2, 4, 4, 5, 3, 4, 3, 3, 3, 3, 4, 2, 4, 2, 3, 3, 3, 3, 2, 1, 3, 3, 3, 3, 5, 4, 3, 4, 4, 3, 3, 4, 2, 3, 3, 3, 4, 2, 2, 4, 3, 4, 4, 3, 2, 3, 2, 4, 3, 2

Open-pollinated yellow dent
C. I. = 2.9
1, 1, 1, 1, 1, 2, 2, 2, 1, 2, 2, 2, 1, 3, 3, 1, 1, 2, 3, 3, 3, 4, 3, 5, 4, 5, 4, 5, 4, 5, 4, 4, 4, 1, 3, 1, 3, 2, 3, 1, 2, 2

Further explanation in the text.



ANDERSON—EAR-TASSEL HOMOLOGIES

TWO COLLECTIONS OF PREHISTORIC CORN TASSELS FROM SOUTHERN UTAH

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The extreme variability of *Zea Mays*, while discouraging to the novice, will make collections of prehistoric maize particularly significant when this variability is at length understood and catalogued. In this connection, it is unfortunate that more well-preserved male inflorescences (corn tassels in common speech) are not represented in archeological collections. While they do not present as many diagnostic features as the female inflorescence (the ear) they are by no means to be despised, particularly since their variation is comparatively easy to measure objectively and exactly. The following account has been prepared partly as a demonstration and partly because these particular collections present features of general interest. Both are from expeditions organized by the Peabody Museum of Harvard University. I am indebted to Dr. J. O. Brew for the opportunity of studying this interesting material and for much pertinent information.

The two collections are roughly contemporaneous and according to current archeological practice in the Southwest would be dated at about 1000 A. D.[1] (see caption fig. 3 for exact citations). One collection consisted of twelve more-or-less perfect tassels from Floating House Ruin on the Arizona-Utah border. The other came from a small cave at Alkali Ridge in southeastern Utah. As illustrated in plate 18, it consists of ten bunches of tassels neatly tied together with a strong withe, apparently of willow bark. The tassels are all just barely ripe; the anthers are developed and little or no pollen had yet been shed. All are neatly laid side by side, pointing the same way. All were either originally trimmed or have subsequently been broken. To a student of maize the most interesting feature of the collection is its comparative uniformity for technical characters, indicating a careful selection of seed stocks on the part of those who grew it. The plant-to-plant variation is no more than is found in such highly selected modern varieties of maize as Golden Bantam sweet corn or the white flour corn of the Hopi. It might be argued that the uniformity is merely a reflection of the innate lack of variability in a widespread primitive variety. On the contrary, such studies of plant-to-plant variation as have been made with Basket Maker maize[2] indicate that it was high.

After the collections had been photographed, the tassels were moistened to make them less brittle and the more-or-less complete tassels were then scored for

[1] Those unfamiliar with the archeology of the American Southwest will find useful summaries in: Roberts, Frank H. Am. Anthrop. n. s. **37**:1-35. 1935; and Bryan, Kirk. Ann. Assoc. Am. Geog. **31**:2; 9-226. 1941.

[2] Anderson, Edgar, and F. D. Blanchard. Am. Jour. Bot. **29**:832-835. 1942.

as many significant features as possible. While to the casual observer the male inflorescence of maize is so featureless as to be of no special interest, it is actually a complicated organ with a very definite ground-plan. The outstanding features are diagrammed in fig. 1, and a complete scoring of the tassel illustrated in plate 19 is presented in text-fig. 2. The maize tassel is built upon a primary axis terminated by the CENTRAL SPIKE (A, fig. 1), along which the spikelets are arranged in many rows (in some South American varieties they are in whorls of 3 or more). Below the central spike are the SECONDARY BRANCHES 'B', 'F', 'G' whose number varies greatly in different races of maize. The lowermost secondaries may bear TERTIARY BRANCHES 'C', and in some South American varieties these may even produce branches of the fourth order. The secondaries may arise

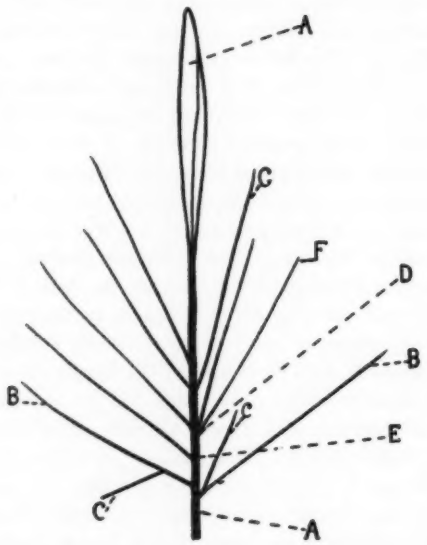


Fig. 1. Diagram showing main features of the male inflorescence (tassel) of *Zea Mays*, with particular reference to the usual type in North America. Further explanation in text.

singly from the main axis or may be in WHORLS (D) of two or more. On the secondaries the SPIKELETS are arranged in pairs, though, as will be shown below, there are departures from this regular arrangement in North American maize. In each pair one spikelet is ordinarily pedicellate and one is sessile, but in North America the pedicellate spikelet may be so subsessile as to be indistinguishable from its neighbor. In South American maize the secondaries often have a long sterile zone at the base of the secondary branches which is without spikelets. In the Southwest and in Mexico this zone is short or is lacking altogether. The

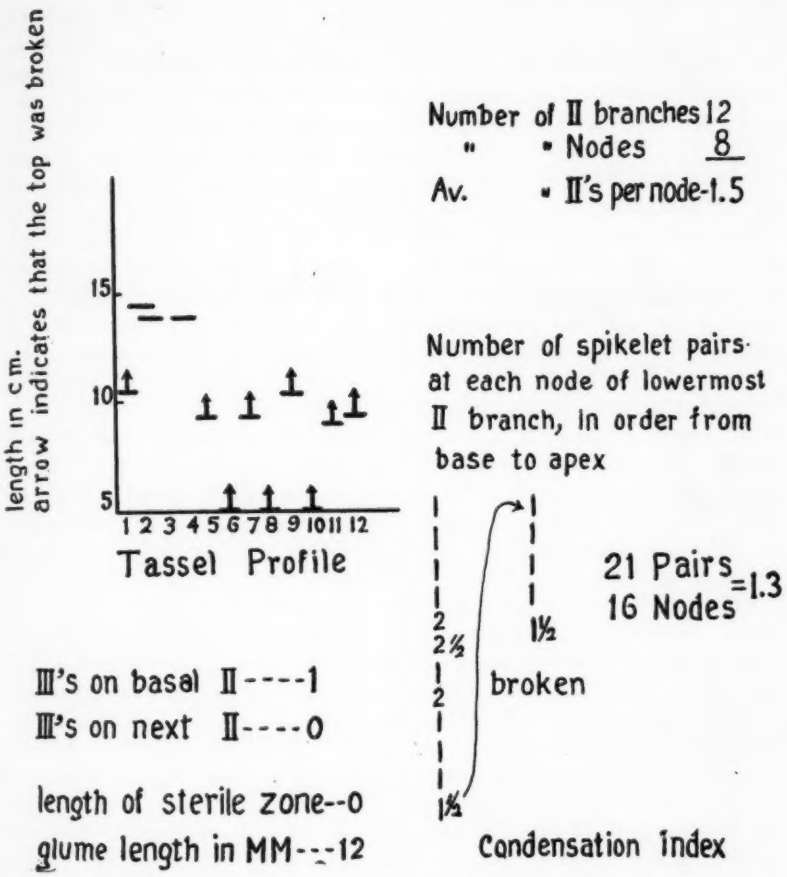


Fig. 2. Score sheet for the actual tassel illustrated in plate 19. Further explanation in text and in Anderson, Ann. Mo. Bot. Gard. 31:325-342. 1944.

length of the spikelets varies between different races of maize, and many of the southwestern varieties have *glumes* (the main feature of the spikelets) which are 12–15 mm. long.

As has recently been demonstrated[3], all North American dent corns show a greater or lesser amount of *condensed* or telescoped internodes in their tassels, and this same condensation (a kind of controlled fasciation) is one of the factors responsible for the higher row number on the ears of these varieties. However this condition may have arisen, it is strongly centered geographically about the Mexico City-Toluca region. Condensed internodes in the tassel of a North

[3] Anderson, Edgar. Ann. Mo. Bot. Gard. 31:325-342. 1944.

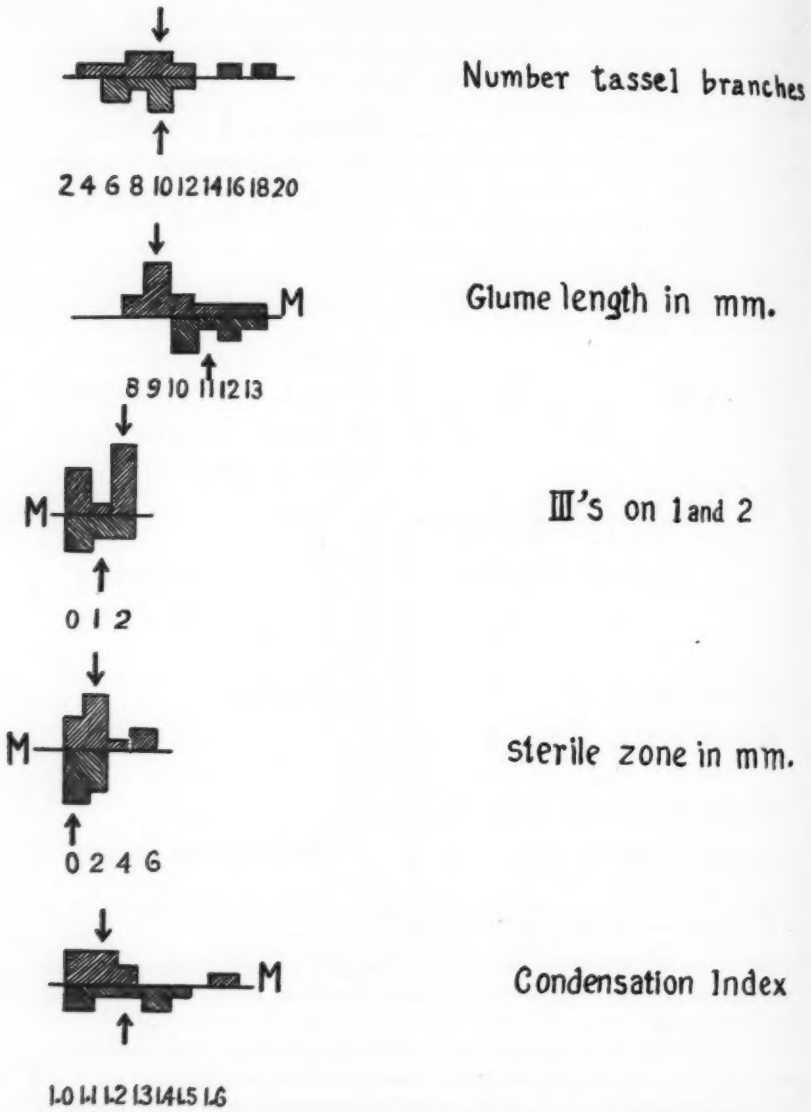


Fig. 3. Frequency distributions for five tassel characters for two prehistoric collections. The two are diagrammed from the same base line: upwards, frequencies for the collection from Floating House Ruin, Peabody Museum, No. 33-62-10/2118 (Room 2A above floor A); downwards, frequencies for the collection from Alkali Ridge, Peabody Museum, No. 33-44-10/3572 (small cave ¼ mi. from site Ab 7–13, Peabody Museum, Southeastern Utah Expedition). "M" represents the direction in which Mexico City tassels would score. Though the two frequencies are similar, the lower set (Alkali Ridge) is slightly more Mexican-like.

American variety of maize therefore imply a connection of some kind with the maize of that area, since high condensation seems to be too complex genetically to have arisen repeatedly. An exact method of scoring this condensation has recently been described[3], and the Condensation Index derived from the tassel permits a fairly accurate estimate of the row number of the ear in North American varieties. The *Condensation Index* is calculated as shown in fig. 2. It is the average number of spikelet pairs per apparent node on the lowest secondary branch (see Anderson, *loc. cit.* for further details). After the Condensation Index the next most significant fact concerning the male inflorescence is the *tassel profile*. This is merely a diagram like the one illustrated in fig. 2. It shows the length of successive secondary branches in order from the base to the apex. In general, it is closely correlated with the size and shape of the ear[3]. In fig. 2, unbroken secondaries are indicated in the profile diagram by a bar, and broken secondaries by a bar with an arrow.

Frequency diagrams for the two collections are shown in fig. 3, the frequencies for *Floating House* being diagrammed upwards and those for *Alkali Ridge* downwards, from a common base line. The arrows indicate the averages (medians) for each of the five characters. There is no difference in the two averages for tassel branch number; for the other four characters there are slight differences. These are scarcely significant statistically, being based upon such small numbers, but biologically they may mean something since they are all in the same direction. For all four characters the Alkali Ridge collection differs from the Floating House series by being slightly more like the maize of the Mexico City-Toluca region. This well-marked geographical type (Mexican Pyramidal of Anderson and Cutler) has long glumes, few tertiaries, an extremely short sterile zone and a very high condensation index. Since the slight differences of the Alkali Ridge collections are longer glumes, slightly fewer tertiaries, a shorter sterile zone and a slightly higher Condensation Index, it seems probable that the Alkali Ridge maize in fact was slightly more Mexican-like than that from Floating House. The difference, if it really existed, was not at all extreme and no more than might be found to-day between the same variety of maize grown in two different Mexican villages.

It is not surprising to find that the maize from the two sites is so similar. They are not far apart in space and were apparently closely contemporaneous. This section of Floating House may be dated as belonging to Pueblo II or Pueblo III, and the Alkali Ridge material as Pueblo I or II. This means that the two sets are within a few hundred years of each other at the most and around 1000 A. D., according to the most widely accepted chronology for the Southwest. Bryan[4] summarizes current opinions on southwestern chronology as follows:

"Pueblo V	1600
Pueblo IV	1300–1600
Pueblo III	1100–1300
Pueblo II	900–1100
Pueblo I	700– 900
Basketmaker III	500– 700

[3] Anderson, *loc. cit.*

[4] Ann. Assoc. Am. Geogr. 31:p. 9.

Basketmaker II	? – 500
Basketmaker I	postulated

Various authorities use slightly different dates, and some question the reality of the boundaries between some of the categories."

The evidence reported above will have greater significance when it can be seen against a background of exact comparisons with various prehistoric and modern collections from the same general area. However, it is in harmony with such facts as have already emerged. The few-rowed primitive flints of the early Basket Makers were apparently gradually tempered by many-rowed Mexican dents which diffused into the "fourcorners" region, *apparently from the north.* (The most extremely "Mexican" collections we have yet seen are those of Scoggins from Yampa Canyon, Colorado, which grade into a group from northern Utah, and the two tassel series described here show even further dilutions of the Mexican influence.) At a later date (1200–1300 A. D.) southwestern maize changed suddenly and radically when long-eared, crescent-seeded types spread into the region, apparently, either directly or indirectly, from the eastern United States[5].

SUMMARY

1. The importance of preserving tassels, as well as the ears, of prehistoric maize is illustrated by two collections from the Peabody Museum.

2. The chief features of a maize tassel are enumerated and methods of scoring the variation exactly are described and illustrated.

3. The tassels from Alkali Ridge were tied together with bark and had apparently been prepared for ceremonial use.

4. The two collections are very similar, the one from Alkali Ridge being slightly more Mexican in its technical characteristics. Both series have such slight plant-to-plant variation as to imply a high grade of agronomic skill on the part of their cultivators.

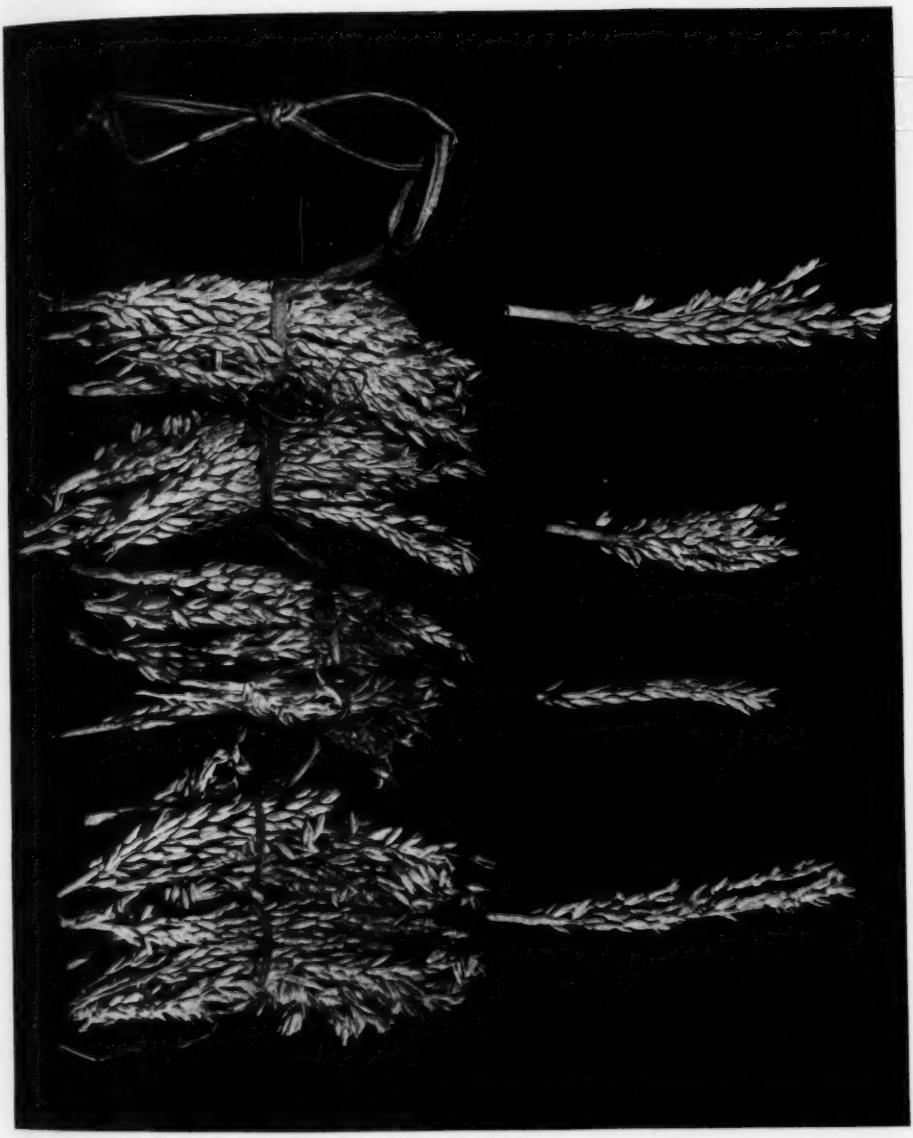
5. The collections are discussed briefly with reference to what is now known of the history of maize in the Southwest.

[5] Carter, George F., and Edgar Anderson. Paper in press.

Explanation of Plate

PLATE 18

Pre-Columbian tassels from Alkali Ridge, Utah. Peabody Museum, No. 33-44-10/3572. Photograph courtesy of the Peabody Museum, Harvard University.

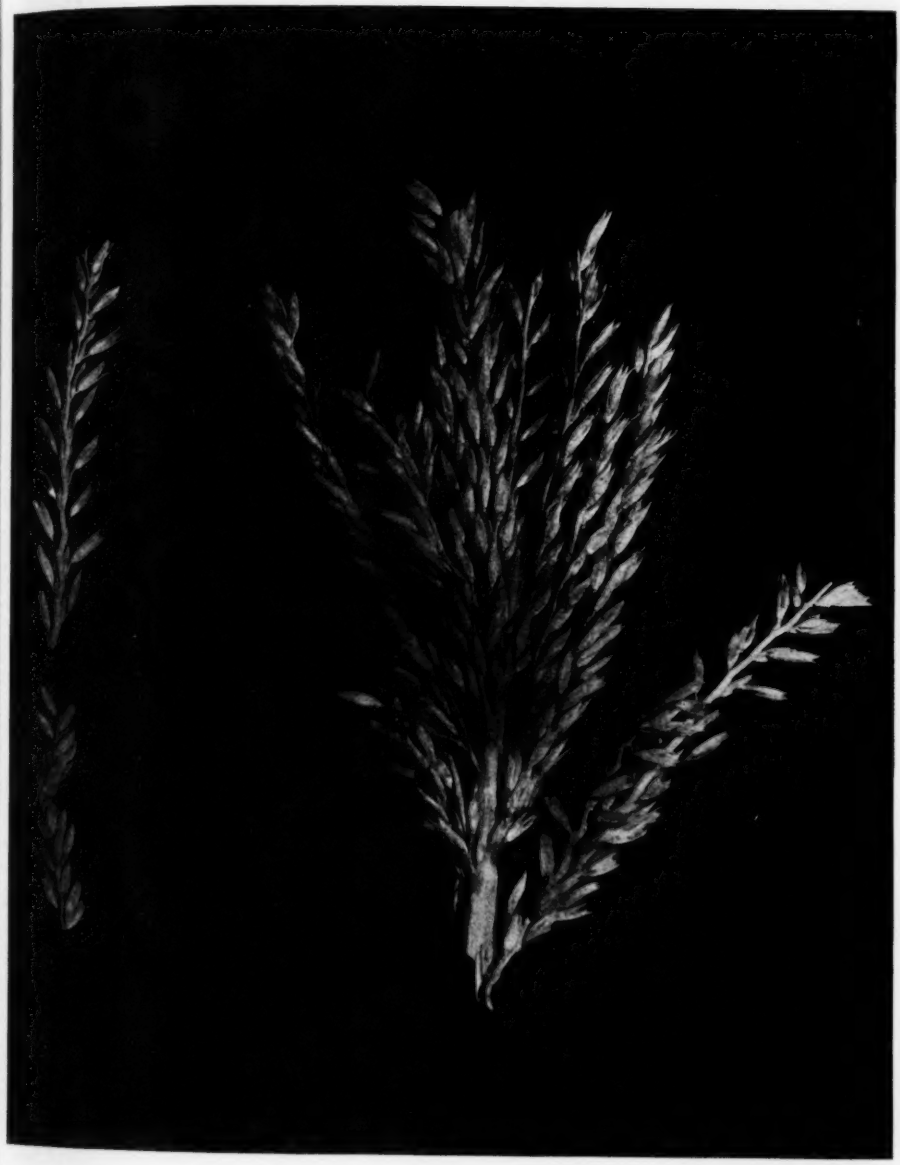


Explanation of Plate

PLATE 19

Tassel and tassel fragments from the band shown in pl. 18: Right: One of the most perfect tassels from the collection, this is scored in detail in text-fig. 2. Left: Fragments from two tassel branches; the upper contains no condensed internodes and the pedicellate spikelets are clearly shown; the lower fragment has subsessile spikelets and a few condensed internodes.

Photograph courtesy of the Peabody Museum, Harvard University.



ANDERSON—PREHISTORIC CORN TASSELS

THE SOURCES OF EFFECTIVE GERM-PLASM IN HYBRID MAIZE

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The last twenty years have seen a complete change in the corn-breeding methods of the U. S. corn belt. Since 1924, when "Copper Cross" was first offered for sale in Iowa[1], hybrid corn has almost entirely supplanted open-pollinated varieties in that area. In the summer of 1944 one could drive across the state without seeing a single field of open-pollinated corn, and in order to find one of any size for study it was necessary to make an intensive search. The total annual yield of hybrid corn in the United States is now about two billion bushels, and the sale of the hybrid seed grosses well over fifty million dollars annually. These are matters of common knowledge to corn breeders but they need to be discussed in terms of population genetics, since the problems they raise are of theoretical as well as practical importance.

In terms of gene combinations and their distributions, the whole genetic pattern of *Zea Mays* in the United States has been catastrophically overhauled in the last two decades. To describe precisely what has happened to the maize germplasm of the U. S. corn belt and to predict its probable effects is a gigantic problem in population genetics. This paper is an attempt to look at the problem as a whole and to give it a preliminary discussion; to estimate some of the facts and to put them on record. Some of these facts are every-day matters to those in the seed-corn business, and it may seem trivial to record them. For some of the others even the estimates must necessarily be so controversial as to be scarcely more than one man's opinion. In gathering the information and discussing its significance I have relied almost wholly upon the staff of the Pioneer Hi-Bred Corn Company. Mr. Raymond Baker, the manager of the breeding department, and his assistants (Messrs. Karl Jarvis, Sam Goodsell, and James Weatherspoon) have put their knowledge and records at my disposal. They also took the trouble to locate Mr. Hershey and obtain the interviews reproduced below. I have done no more than to phrase the problem and to write the paper. If the conclusions, however, are out of line with the actual facts, the fault is entirely my own.

Before discussing gene-pattern distributions it will be necessary to describe the method of producing and marketing modern hybrid seed corn for those unfamiliar with the process. Maize is normally open-pollinated and the plants under such conditions are highly heterozygous. In producing hybrid corn, uniform inbred lines are produced by controlled self-pollinations or sib-pollinations until practical homozygosity has been reached (usually six or more generations). Most of the inbreds produced in this way are discarded or eliminate themselves by their sterility. The few which remain are tested in crosses with each other until sets

[1] Iowa Seed Co. Catalogue. 1924, p. 30.

of four inbreds are obtained which make an effective "four-way" cross. (Single crosses and top-crosses are also produced but the bulk of the business is now in four-way crosses.) Let us designate the four in any one cross as 'A', 'B', 'C', and 'D'. 'A' and 'B' are crossed together the first year in one plot (by detasseling, i. e., removing the male inflorescence from one parent) and 'C' and 'D' in another. The following year hybrid 'AB' is interplanted with hybrid 'CD'. The present practice is usually to have this done under contract by skilled farmers, who detassel either 'AB' or 'CD', as the case may be, and the resulting crop ('AB' x 'CD') is marketed as seed corn. A large part of the effort in modern corn breeding is spent in maintaining and improving the inbred lines upon which the business is based. In addition to the purely negative effort of roguing, the development of "Convergent Improvement" by Richey and Sprague[2] has resulted in what are termed in the trade as "second cycle" and "third cycle" inbreds. These are produced as follows: Let us suppose that inbred 'XYZ' is useful in a particular set of crosses except that it has certain obvious faults. It might, for example, have such weak roots or short ears that even its hybrid offspring are affected; or it might, on the other hand, be so weak as to be difficult to raise in quantity year after year. In a convergent improvement program 'XYZ' is therefore crossed with a series of other inbreds (or with an open-pollinated variety) and the resulting hybrids are backcrossed to 'XYZ' again. From these three-quarter bloods, by inbreeding and selection, a series of second-cycle inbreds is obtained, and if the work has been well done at least one of them may have most of the advantages of 'XYZ' without all of its defects.

Such is the present system. By it, effective gene combinations are discovered in the breeding plots of the experiment stations and corn-breeding companies and are propagated for sale to the actual farmer. Where did these gene combinations come from on the whole? Do they trace back to many open-pollinated varieties or to a few, and how does the present process of obtaining effective gene combinations compare with that in vogue before the hybrid-corn business came into being? To obtain an approximate answer to these questions 6 widely sold four-way hybrids of known composition were listed. They are all outstanding commercial successes and have been very widely planted. They might, in one year or another, have accounted for one-quarter of the total corn crop in central Iowa. Since all are four-way crosses we might have expected as many as 24 inbred lines; actually only 18 are involved, the inbreds known as Ill A, Iowa 205, R-4, Wf-9, and Ill-HY having entered into two or more crosses. When the 18 inbreds are tabulated according to the open-pollinated variety from which they were derived, we find the whole group came from only 3 open-pollinated varieties! Twelve are from some strain of Reid Yellow Dent, 3 from Krug, and 3 are from Lancaster Surecropper, as follows:

[2] Richey, Frederick D., and George F. Sprague. Experiments on hybrid vigor and convergent improvement in corn. U. S. Dept. Agr., Tech. Bull. 267:1-22. 1931.

REID YELLOW DENT: HY, 38-11, WF-9, Os 420, Os-426, Ia 205, R-4, Ill A, Idt, Ind Fe, TEA, LE-773.

KRUG: K-77, K-187, K-159.

LANCASTER SURECROPPER: L-317, L-289, LDG.

The way in which the inbreds are combined is also significant. The six four-way hybrids under consideration were combined as follows:

3 hybrids: 3 Reid inbreds and 1 Lancaster inbred.
1 hybrid: 2 Reid inbreds, 1 Lancaster inbred and 1 Krug inbred.
1 hybrid: 2 Reid inbreds and 2 Krug inbreds.
1 hybrid: 4 Reid inbreds.

The above estimate is from only one section of the corn belt but it is in line with what is generally known. The bulk of the inbreds now being most widely used were derived from very few open-pollinated varieties. In the above sample only 3 open-pollinated varieties were represented—Reid Yellow Dent, Lancaster Surecropper, and Krug. The last of these is little more than a sub-strain of Reid. According to Wallace and Bressman[3], it was originated by George Krug of Woodford, Illinois, who crossed Gold Mine with a Nebraska strain of Reid and selected for a smoother rather small-eared utility corn.

We are faced with the remarkable fact therefore that much of the corn now being grown traces back mainly to two open-pollinated varieties. It is not surprising to find Reid inbreds high on the list since that variety in one sub-strain or another dominated the corn belt when hybrid corn was being evolved. Popularity might also help to explain the prevalence of Krug inbreds, this variety having been very extensively grown in the central corn belt immediately before the advent of hybrid corn on a commercial scale. However, these were by no means the only varieties grown commercially at that time. As late as 1906, when E. M. East was just starting his work with inbreeding, 11 varieties of yellow dent corn were offered for sale by the Iowa Seed Co. in Des Moines. The standard authorities on corn growing, Wallace and Bressman[3], in 1937 listed the following open-pollinated yellow dents as commercially important in the central corn belt: Reliance, Leaming, Gold Mine, Ioleaming, Golden King, in addition, of course, to Reid and Krug. Some of these are known to have been inbred fairly extensively, yet only the Reid and Krug inbreds have held up under commercial competition. Popularity of the open-pollinated variety certainly would not explain the success of Lancaster Surecropper inbreds. This variety was of such minor importance in the corn belt that Wallace and Bressman merely list it among the "also-rans" without any further comment. It was not until its inbreds demonstrated their usefulness that it became a real factor there. Its excellence as a source of good inbreds is well known among corn-breeders. In addition to the inbreds listed above a number of other excellent ones have been derived in whole or in part from

[3] Wallace, Henry A., and Earl N. Bressman. Corn and corn growing. New York. 4th ed. 1937 (see p. 208).
[3] *loc. cit.*

this variety, and Dr. F. D. Richey informs me that at least three well-known inbred lines came from a single open-pollinated ear of Lancaster Surecropper. It is also generally appreciated that the inclusion of a Lancaster inbred in a four-way hybrid steps up productivity, and it will be noted that half of the hybrids listed above were so constituted.

It is apparently true therefore that the inbred strains in use at the present time are far from a random sample of the open-pollinated varieties which immediately preceded them. Many of the minor varieties of yellow dent are not represented by inbreds derived from them. The germ-plasm of two open-pollinated varieties predominates in modern inbreds, and one of these varieties, Lancaster Surecropper, is represented out of all proportion to its previous importance in this region. If these phenomena are general and not merely a chance result, they raise a number of interesting questions. A few of these can be suggested here: (1) If Lancaster Surecropper is really an especially effective source of good inbreds is there anything in its history to suggest why this might be so? (2) How do the frequency and the pattern of effective gene combinations in hybrid maize compare to those in the open-pollinated varieties? How much of the apparent progress is merely the uncovering of progress already achieved by the originators of Reid, Krug, and Lancaster Surecropper? Is potentially effective germ-plasm being lost under the present system?

To question number 1 we can give a partial answer. Lancaster Surecropper was originated in Pennsylvania by Mr. Isaac Hershey and his father. The former is still living, and Mr. Karl Jarvis and Mr. James Weatherspoon of the Pioneer Hi-Bred Corn Company visited him in September of this year and have kindly prepared accounts of the interview. Mr. Jarvis's is printed in its entirety; supplementary and confirmatory evidence from Weatherspoon's report is given in brackets:

> In 1860 (when Isaac Hershey was eight years old) a neighbor, Henry High of Byerstown, Lancaster Co., Pa., received a packet of a variety of corn from the Patent Office. Mr. High and several of the neighbors liked this new variety and some of them, especially Jacob Hershey (Isaac Hershey's father) and Jacob's brothers, began to depend on it for their main crop. It was described as a rather small, rather slender-eared corn, very variable in type [but a good yielder]. In general, it was rather smooth, mainly one-eared, and rather early. From Mr. Hershey's description I got the impression that it must have been either a semi-flint or else a flint-dent hybrid which was still segregating. One of the common segregates was a "lilac colored" ear, which caused one of Isaac Hershey's uncles to nickname it "Lilac corn."
>
> The common corn of the community was a large, late, rather coarse type with medium to rough kernels, rather resembling Golden Queen according to Mr. Hershey. The new variety, "Lilac corn," was such a contrast and looked so much smaller, even though very productive, that most farmers laughed at it and called it "popcorn." The Hersheys began selecting later strains and blending in a little seed from a few selected ears of the larger, later and rougher local varieties. This blending process, which Isaac Hershey called "dipping," was repeated a number of times [by his father] before Isaac started farming, but he does not know just how many times. Isaac estimated that he himself had "dipped" Lancaster Surecropper six or eight times with various varieties including once with some white corn. "Dipping" consisted of taking two or three selected, high-yielding ears, shelling them, and then mixing the seed thoroughly throughout his pile of shelled seed corn. The last dip was about 1910.

One year, Isaac Hershey planted a field to Golden Queen. The stand was very poor so he replanted with Lancaster Surecropper. Since he saved some seed corn from this field, he undoubtedly introduced considerable Golden Queen into his variety. In addition, after his neighbors began to get seed from him and then grow their own strains, Isaac Hershey would watch their fields and when a strain had been carried on for eight to ten years and seemed to be desirable, he would buy back about one-half bushel of selected seed and blend it into his own.

At first there was no attempt to make the variety uniform. In fact, if anything, they (Isaac and Jacob, and Noah, son of Isaac) preferred to keep it "mongrelized." In seed selection, in general, he preferred a medium-length ear, but would save any ear irrespective of type which was, as he said, "a good business ear that would put lots of pork on a hog." He insisted on well-matured, sound ears with clean shanks and no mold or "silk cut." He said he could recognize the latter by slightly protruding kernels. This insistence on a sound, well-matured ear earned it the name of "Surecropper," since it always matured while other later, softer varieties did not. [He did pick ears with good solid, clean shanks, evidently ears with a reasonable amount of length. In regard to length, he did say this—that he kept an ear for seed if it was somewhat short, provided that the kernels were not filled out clear over the end. He seemed to think if there was still bare cob sticking out at the end the ear still had considerable chance to develop more length. However, if it was a short ear and filled out to the end, he believed there wasn't any possibility of getting any length out of it.] No plant type selection was made because, "I never saw a good ear of corn on a poor corn plant." His only regret was that this type of selection had given a weak-rooted variety. However, his son, Noah Hershey, had later selected for a larger ear and a better root system by making field selections.

When Lancaster Surecropper became popular and seedmen began buying seed from Mr. Hershey, they continually put pressure on him to select for uniformity and a longer, more showy ear type. He refused at first, but finally gave in, and, as he said, "spoiled Surecropper and cut off about 10 to 15 bushels per acre at least." This "spoiling" occurred about 30 years ago. Some years ago Pennsylvania State College asked him to select a sample of Lancaster Surecropper representing the original range of types as he originally grew the variety, before he "spoiled" it. This was done and sent to them and may possibly still be stored somewhere at State College. [In the early days with the development of Lancaster Surecrop, Hershey didn't go in for selling seed very much. He was mostly interested in a high-yielding corn. However, as the fame of his corn spread seedmen wanted to sell Lancaster Surecropper, but they, of course, insisted that he dress the corn up—that is, select for uniformity of ear type. So, along about 1910, he began to sell quite a bit of seed and he stopped "dipping" his corn and began to select for uniformity. He feels very strongly himself that at this stage he began spoiling his corn. In fact, he said that he wrote to a worker in the U. S. D. A. and told him how he spoiled Lancaster Surecrop, and that was by selecting for uniformity as to ear type and dressing it up to suit the seedsmen.]

Incidentally, Mr. and Mrs. Hershey mentioned as a very profitable year one in which they sold 1,000 bushels of seed at $3.00 per bushel. For super-select seed such as he himself would plant, the charge was $5.00 per bushel. Since ordinary corn was bringing 50 to 60 cents per bushel at that time, they were very glad to get such prices. At various times Lancaster Surecropper was shipped to Europe, China and frequently to South America so its germ-plasm may well be scattered throughout the world.

Mr. Hershey's opinion of the bad effects of selection for uniformity is interesting because it parallels conclusions reached from a morphological study of recombination in species crosses[4]. From both theoretical and experimental considerations it was shown that the achievement of optimum recombinations in crosses between species or races is a difficult and long-time affair. Relatively little progress can be made in any one generation. The practical problem involved is to be able to work towards the desired end, generation by generation, without losing potentially valuable genes before they are incorporated with the other superior ones. In the paper referred to, it was suggested that simultaneous selection for performance and for morphological diversity might solve this dilemma. It is interesting to find that a family of successful corn-breeders has come to

[4] Anderson, Edgar. Recombination in species crosses. Genetics 24:668-698. 1939.

rather similar conclusions on the basis of practical experience. It should be possible to test these conclusions experimentally. Parallel convergent improvement experiments[5] could be set up with and without selection for morphological diversity during the generations of selection and inbreeding. If Mr. Hershey and I are right a more complete synthesis of desirable genes could be achieved by considering the general morphology of the plants chosen as parents in each generation as well as their performance. (See Anderson, *loc. cit.*, pp. 694-695, for a more complete discussion.)

The second set of questions (concerning the pattern of gene combinations) cannot be answered at the present time, nor have I found any general unanimity of opinion among maize breeders or maize geneticists. We know virtually nothing about the breeding structure (or, to put it in other words, the population genetics) of a field of maize. On this fundamental subject almost nothing has been written. The title of Shull's pioneer paper[6] defined the problem but his discoveries helped to initiate four decades of more pressingly practical research. Jones and others have shown that mating is not at random in open-pollinated fields[7]. One can scarcely visit a maize-breeding farm without noticing a number of very suggestive phenomena which bear on the problem, yet at present we are almost without facts. We do not even have a simple plant-by-plant description of a single field of any open-pollinated variety, let alone an estimate of how the individuals of one generation are related genetically to those of the next. Yet before we can give reasoned answers to such questions as those raised above, we must have fairly reliable estimates on these matters.

To achieve optimum results with hybrid-corn breeding we must understand at least approximately the population genetics of a field of open-pollinated maize. We shall have to move swiftly if the desired information is to be recorded; open-pollinated fields are almost a thing of the past. It may be necessary for breeders of hybrid corn to subsidize highly skilled farmers as raisers of open-pollinated corn until we have at least an estimate of when, where, and how the majority of the useful gene combinations in hybrid corn were accomplished.

SUMMARY

1. An attempt was made to determine which open-pollinated varieties of maize have contributed most germ-plasm to modern four-way hybrids.

2. For central Iowa it was shown that one group of highly successful hybrids was made up wholly of inbreds from three open-pollinated varieties, Reid, Krug, and Lancaster Surecropper.

3. Evidence is given for the particular excellence of this latter variety as a source of hybrid germ-plasm. The history of the variety was obtained from Isaac

[5] Richey and Sprague, *loc. cit.*

[6] Shull, George H. The composition of a field of maize. Amer. Breed. Assoc. Rept. 4:296-301. 1908.

[7] Jones, D. F. Selective fertilization. 163 pp. Chicago. 1938.

Hershey, one of the originators, and his methods of selection are described.

4. Two questions are discussed in the light of the above information: (a) the possible advantages of selecting simultaneously for performance and morphological diversity; (b) the need of more exact information on population structure in *Zea Mays*. It is concluded that, for the sake of understanding and improving modern hybrid maize, it will be necessary to investigate the breeding structure of representative open-pollinated varieties.

NOTES ON SOME NORTH AMERICAN ASCLEPIADS

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For nearly ten years I have been engaged more or less actively in a revision of the species of *Asclepias* in the United States. The problem has been complicated and its completion delayed by a number of factors, particularly the need of delineation of the genus with respect to the other American genera of Asclepiadaceae. World War II brought its own complications, all too familiar to any systematist, in this case the chief of which was the enlistment in the "Seabees" of Albert A. Heinze, long my collaborating illustrator. With the indefinite duration of these hindrances in mind, I have thought it best to publish occasional novelties; I now offer some notes concerning the nomenclature and identity of a few of our North American Asclepiads, not only because they should have been discussed long ago, but because I intend to publish in the near future some observations on their geographical variation.

ASCLEPIAS MEXICANA HBK. VS. *A. FASCICULARIS* DCNE.

One of the most frequent Milkweeds of our western states is "*Asclepias mexicana*" of nearly all American authors, which ranges roughly from Idaho to Nevada and westward to the Pacific Coast. It is a member of the *incarnata*-alliance of the subgen. *Euasclepias*, having narrowly stipitate gynostegia, whorled leaves, and paired or clustered inflorescences at the upper nodes. The flowers are grayish-pink to white, and, as is usual in this alliance of the subgenus, offer few structural peculiarities indeed, the only one coming to mind at the moment being the attachment of the corona horn usually at the middle, rather than at the base, of the hood.

Apparently the best diagnostic characters of the species, again as is usual in its alliance, are found in the leaf-branch system. The phyllotaxy is particularly notable, that upon the main stem and flowering branches being predominantly ternate, but occasionally quaternate or even opposite. In addition to the flowering branches of normal size, the species is distinguished usually at a glance by means of dwarf axillary branches which do not flower as a rule and lend to the plant a somewhat "heterophyllous" aspect because of their usually smaller, predominantly opposite leaves. In any case, the stems and branches are either glabrous or inconspicuously and generally pubescent, without the appearance of pubescent "lines" which will be discussed presently in other connections. This species may well extend northward into southern British Columbia and southward into Baja California, although the herbarium of the Missouri Botanical Garden has no supporting evidence.

Issued November 30, 1944.

"*Asclepias mexicana*" of the western United States invariably is credited to Cavanilles (Ic. 1:42. *pl. 58.* 1791), and an examination of the original description and illustration alone might not appear to bar such an interpretation. The former, as one might fear, is somewhat vague, and conveys as its most important clues that the leaves of the plant are whorled and about three inches long by three lines broad. The illustration is rather conventional in the antique manner, and shows 5–6 lance-elliptic leaves in a close whorl, without axillary branches, and with highly generalized inflorescences. No locality is cited by Cavanilles, although a majority of his Mexican species are known to have been collected in the mountainous districts in the vicinity of Mexico City (as in the case of *A. Linaria*, "*prope Mexico et Chalco*"), and there is some justification for the assumption that his *A. mexicana* might well have been from the same region.

As a matter of fact, this assumption virtually is proved by the Mexican exsiccatae labelled "*A. mexicana* Cav.," a fair number of which occur in American herbaria. Attention is first directed to such specimens in the herbarium of the Missouri Botanical Garden when it is noted that they came not from districts contiguous to the distribution of "*A. mexicana*" in the western United States, but from the southern and eastern Mexican states of Nuevo Leon, Mexico, Oaxaca, and the Distrito Federal. Comparison with the large suites of the West Coast "mexicana" proves the two populations to represent distinct species.

The Mexican species at first glance is of a much "neater" habit, and upon only one specimen of the nine before me is there any indication of the dwarf axillary branches so characteristic of the West Coast species. The leaves are in much closer, more uniform whorls of 4, or very rarely 5, never 3, individuals, and they are of somewhat coriaceous or fleshy texture as evidenced by their revolute margins, a character that I have never observed in the plants of the United States. The stems of the Mexican species may be glabrate below, but in the upper portion they are marked by four pubescent lines decurrent from the bases of the leaves. The importance of these lines will be stressed further in another connection. The flowers of the Mexican species are disappointingly similar to those of the western United States, as might be expected, and the only technical distinction that I have noted is a strong tendency for the corona horns of the Mexican species to be inserted at the base of the hood, whilst they are inserted at about the middle in the species of the United States.

After such considerations, a return to Cavanilles' plate will convince most readers that the pioneer Spanish botanist had before him, in fact, not the species of the western United States, but that of southern and eastern Mexico! Nor is one in want of a name for the northern species, for *A. fascicularis* Dcne. (in DC. Prodr. 8:569. 1944), based upon a collection by Douglas (in "*Nova California*"), immediately is available, although the original description, again, is quite noncommital. In "New California" Douglas could have collected but one Milkweed with verticillate leaves.

ASCLEPIAS GALIOIDES HBK. VS. *A. SUBVERTICILLATA* (GRAY) VAIL

Because of its poisonous properties, stockmen throughout the western plains of the United States, from Nebraska to Texas and westward to Idaho and Arizona, usually are familiar with the plant widely known as "*Asclepias galioides* HBK.". This species closely resembles the frequent *A. verticillata* L. of the East from which it is distinguished, occasionally with some difficulty, by means of its more extensive taproot system and tendency to the production of dwarf, microphyllous, axillary branches similar to those of the closely related *A. fascicularis* Dcne. As in the latter species also, the leaves of this plant are predominantly ternate, but occasionally 4–5-nate or opposite, particularly above and upon the microphyllous dwarf shoots. Because of the variability of the leaf whorls, Dr. Gray proposed for certain of these plants the name *A. verticillata* var. *subverticillata* (Proc. Amer. Acad. 12:71. 1876), which was raised to specific rank by Miss Vail in 1898 (Bull. Torrey Club 25:178). In my studies I have made every effort to distinguish *A. subverticillata* from the commonly recurrent "*A. galioides*", but, because of the general variability of the population as a whole, have come to the conclusion that they are not even varietally distinct.

Asclepias galioides, as originally described by Kunth (HBK. Nov. Gen. & Sp. 3:188. 1819) was based upon a Mexican plant collected "*inter Valladolid de Mechoacan et lacum Cuiseo*" (*Bonpland 4304* in Hb. Paris or Berlin), which is unavailable to us at present and may be permanently lost. No illustration accompanies the text, and the description as a whole is scarcely definitive with the exception of the brief introductory diagnosis: "*A. caule suffruticosa, ramoso, quadrifariam piloso; foliis quaternis, subsessilibus, erectis, linearibus, margine revolutis, uninerviis, glabris, ... folia . . . . 2–2½ pollices longa, 1–1½ lineas lata.*"

Here, at least, is a definite geographical citation, from the highlands of Michoacan, with a critical description of the stem and foliage. If we now turn to the herbarium of the Missouri Botanical Garden, we find that there are two elements amongst the Mexican specimens labelled as "*A. galioides.*" More numerous are plants from the north-central plains and foothills of Chihuahua, Coahuila, Durango, and northwestern San Luis Potosi, which agree perfectly with the plants of the adjacent plains of the United States, having predominantly ternate leaves 0.1–0.3 cm. broad and stems which are either glabrous or with two decurrent lines of pubescence. But amongst the lot are three specimens from the high Sierra Madre Oriental of Nuevo Leon (*Muller & Muller 248*), San Luis Potosi (*Parry & Palmer 584*), and Mexico (*Hahn s. n.*) which obviously would have been distributed as *A. mexicana* but for their quaternate slightly narrower leaves (0.2–0.5 cm. broad), and stems which also show plainly the four pubescent lines characteristic of typical *A. mexicana* as represented by our collections, and as noted by Kunth. Since a "Paris line," probably intended by Kunth, equals 2.325 mm., it is fairly obvious that the true *A. galioides* HBK. is only an intergrading

narrow-leaved phase of *A. mexicana* Cav., the lance-elliptic leaves of which vary from 0.3 to 1.0 cm. broad upon the basis of our present representation. The proper designation of "*A. galioides*" of the plains of the west-central United States and adjacent north-central Mexico, therefore, is *A. subverticillata* (A. Gray) Vail.

THREE SUBSPECIES OF ASCLEPIAS TUBEROSA

One of the most beautiful and familiar Asclepiads of the United States is the commonly orange-flowered Butterflyweed, the inclusive species *A. tuberosa* L., which ranges roughly from Massachusetts to peninsular Florida and westward to Colorado and Arizona. The plants commonly assigned to *A. tuberosa* are notoriously variable, and it is not unnatural that there are two opposed views concerning them.

The less conservative view is that of the late Dr. John K. Small, who was able to recognize three specific entities in the complex and keyed them as follows in his 'Flora of the Southeastern United States' (ed. 1, p. 941. 1903):

Hoods linear-oblong or linear-lanceolate, the interior folds meeting the margins near the apex; calyx-lobes barely ⅓ as long as the corolla-lobes.
- Leaf-blades oblong, obtuse: follicles slender-fusiform — 1. *A. decumbens*
- Leaf-blades lanceolate-oblong or linear-lanceolate, acute or rarely obtuse; follicles fusiform — 2. *A. tuberosa*

Hoods broadly oblong, the interior folds vanishing remote from the apex; calyx-lobes nearly ½ as long as the corolla-lobes — 2a. *A. Rolfsii*

In the text, Dr. Small indicated the distribution of *A. decumbens* L. as, "In dry fields, New York, Ohio and Illinois to North Carolina and Florida. Occurring also probably elsewhere further north"; that of *A. tuberosa* L. as, "In dry fields, Maine to Ontario, Minnesota, Colorado, Florida, Texas and Arizona"; and that of *A. Rolfsii* Britton as, "In pine lands, southern peninsular Florida."

The second edition of Small's 'Flora' treats the complex precisely as in the first. However, his 'Manual of the Southeastern Flora' (p. 1068. 1933) presents a surprisingly different key for the same three species:

Leaf-blades acute or acutish, lanceolate or lance-elliptic: horn very slender.
- Calyx-lobes ⅓ the length of the corolla-lobes or less; hood narrowly elliptic — 1. *A. decumbens*
- Calyx-lobes nearly as long as the corolla-lobes: hoods obovate — 2. *A. tuberosa*

Leaf-blades obtuse and broadly rounded, pandurate; horn very stout — 3. *A. Rolfsii*

The distributions are somewhat altered as follows: for *A. decumbens*, "Dry fields, various provinces, Fla. to Tex., Ill., and N. Y., probably also further north"; for *A. tuberosa*, "Dry fields, various provinces, Fla. to Tex., Ariz., Minn., Ont., and Me."; and for *A. Rolfsii*, "Pinelands, Coastal Plain, Fla. to S. C.". Perhaps the chief impression to be received from Dr. Small's two treatments of our problem might be summarized as considerable uncertainty regarding morphological criteria, and suspiciously coincident geographical distributions, particularly of *A. decumbens* and *A. tuberosa*.

The more conservative view of the *A. tuberosa* problem recently has been expressed very forcibly in a letter to me by Professor M. L. Fernald, which I wish to quote:

"In my own work and in the treatment of the genus for the Manual, I have found it impossible to draw any geographic or morphological lines in *A. tuberosa* except for possibly minor forms. The type, of which I have a photograph, of *A. tuberosa*, that is, the specimen in the Linnean Herbarium when he prepared Species Plantarum and which was marked by him K [Kalm] *tuberosa*, has oblong leaves broadly rounded or auricled at base and somewhat clasping. We have no photograph of the type of *A. decumbens*, but that was a Virginian plant, presumably based on a Clayton specimen (Gronovius) from a region where Clayton could have collected almost anything in the group.

"As I look over our material, and as I know intimately the plant in eastern Virginia, it is heteromorphic, and one can get any color that he wishes to collect, from the ordinary plant with vivid orange hoods and reflexed carmine perianth to others with the hoods red, and others with them pale to bright yellow, and others with hoods and perianth bright yellow. These color-variations which are helter-skelter, occur on plants with strongly ascending stems or others with the stems lopping while the leaves may be anything from broadly rounded at base and subclasping to subcuneate at base in the same or adjacent patches. They may be narrowly ovate, narrowly oblong, oblong- or linear-lanceolate, round-tipped or acute and, as I said, I have personally abandoned all hope of getting any tangibility into the series. It is certainly not divisible into one lot growing (as you express it) north and west of the Ohio, as contrasted with others growing farther south and east, for on the coast from New England southward we can find plenty of specimens with broad-based leaves to match the most extreme plants farther west, while from Michigan, Indiana, or Minnesota we can find plenty of specimens with the leaves as narrow and oblong as in the more extreme plants of the Atlantic states.

. . . . . .

"Certainly the type of *A. tuberosa* is easily matched both east and west. Coming from Kalm, it naturally did not come from north or west of the Ohio, but presumably from New Jersey or eastern Pennsylvania, for Kalm had his headquarters in that vicinity. And *A. decumbens*, if it was anything more than a form, was from decidedly an eastern area, where anything within the group can be found."

Professor Fernald refers to my view expressed in a previous letter to him soliciting his opinion, which was freely given as quoted. My observation had been, simply put, that the leaves of *A. tuberosa* from roughly north of the Ohio and west of the lower Mississippi Rivers are generally broadest below the middle, while those east and south tend to be broadest above the middle, although this population also contains many of nearly oblong or elliptic outline. The western population also may be said to have the leaf base predominantly truncate or cordate, while the eastern population varies from narrowly cuneate to somewhat cordate, as Professor Fernald testifies. In Florida, a third population occurs, currently known as *A. Rolfsii*, in which the leaves tend to be broadest above the middle, but usually more or less conspicuously hastate at the base, although rarely cuneate as in the more northern plants.

In the material of *A. tuberosa* generously lent for my study by the Gray Herbarium, I was very interested to find a sheet from the herbarium of Dr. Gray upon which are pasted two separate collections in the manner commonly employed in former times. The specimen to the right was collected by Oakes at Plymouth, Mass., and shows the oblong-oblanceolate, broadly acute leaves to good advantage; the specimen to the left was collected by an unspecified person at Columbus, Ohio, and shows the broadly ovate-lanceolate leaves commonly found in the Midwest. In the extreme lower left corner of the sheet, Dr. Gray had affixed a label bearing the annotation "*Asclepias tuberosa* L.", and another label directly beneath the plant from Ohio bears the designation "var. *decumbens*". The latter annotation can have little claim to validity as typifying the proper nomenclature for the western population, since *Asclepias tuberosa* var. *decumbens* (L.) Pursh (Fl. Amer. Sept. 1:182. 1814) indisputably was provided for Virginian plants "with the

stems lopping" as discussed by Dr. Fernald in his letter.

It should be emphasized that the three populations noted by me are radically different from the three of Dr. Small in that their ranges do not overlap extensively, much less coincide. Furthermore, I have not been able to observe any significant morphological characters distinguishing the three species as noted by Small; his calyx lobe-corolla lobe ratios particularly have proved to be unreliable. The problem as I see it principally concerns leaf variation.

At this point we should examine the basic nomenclature of the three populations that I have observed. That of *A. Rolfsii* may be disposed of easily, since it is a modern species based upon a specimen deposited in the herbarium of the New York Botanical Garden and collected by the late Dr. N. L. Britton at Miami, Fla. This plant bears the more or less hastate leaves characteristic of the vast majority of the peninsular population. Concerning the Linnaean *AA. tuberosa* and *decumbens,* I can best refer again to Professor Fernald's letter, since the receipt of which I have been allowed to examine the photograph he mentioned. The leaves of this "type" of *A. tuberosa* in all respects are similar to those of the eastern population as a whole, being oblong-oblanceolate, distinctly widest above the middle, broadly acute to obtuse at the tip, and gradually tapering to a narrow truncate or obscurely auriculate base. Professor Fernald's observations concerning the variability of the stem posture of the eastern population are particularly valuable in disqualifying that specific character ascribed to *A. decumbens* by Linnaeus.

All this, of course, leaves the western population without a specific name, unless I again have overlooked an obscure reference in Rafinesquiana. Nor do I find an appropriate varietal designation, although a few adjectives for color-forms have been proposed. I am proceeding to describe all three populations as subspecies, a category in great disuse if not misuse amongst contemporary plant systematists.

ASCLEPIAS TUBEROSA ssp. **tuberosa** Woodson, nom. nov.

Asclepias tuberosa L. Sp. Pl. 217. 1753.
Asclepias decumbens L. loc. cit. 216. 1753.
?*Asclepias revoluta* Raf. Fl. Ludov. 51. 1817.
Asclepias Floridana Lam. Encycl. 1:284. 1783.
Asclepias tuberosa var. *flexuosa* James, in Bot. Gaz. 13:271. 1888.
Acerates Floridana (Lam.) Hitchc. in Trans. Acad. Sci. St. Louis 5:508. 1891, as to name-bringing synonym only.

ASCLEPIAS TUBEROSA ssp. **Rolfsii** (Britton) Woodson, stat. nov.

Asclepias Rolfsii Britton, apud Small, Fl. Southeast. U. S. ed. 1. 943. 1903.

ASCLEPIAS TUBEROSA ssp. **interior** Woodson, ssp. nov. Plantae speciei habitu inflorescentiaque congruentes, in regione typica i. e. praecipue in planitiebus centro- et austro-occidentalibus foliis basim versus plus minusve latioribus semper ferme varie ovatis vel lanceolatis apice sensim acuminatis basi plerisque plus minusve cordatis vel non rare truncatis, ad regionem orientis i. e. prope fl. Ohiense et Mississippiense inferiore regioni ssp. tuberosae adjacentes ibique foliis saepe fere

oblongis vel ellipticis apice acutis nisi fere obtusis basi minus frequenter cordatis non rare fere cuneatis. — Exemplum typicum: IOWA: CLAY: level moist prairie six miles north of Ruthven, Sept. 4, 1944, *A. Hayden 3195* (Herb. Missouri Bot. Gard., TYPUS).

Although intergrading specimens will constitute a recurring nuisance, as is to be expected in subspecies occupying contiguous ranges, the following key should be of some help in identifying specimens of the three subspecies:

Leaves typically obovate to linear-oblanceolate, i. e. broadest above the middle, intergrading to oblong and elliptic, particularly westward, the apex chiefly broadly acute to obtuse or rounded, the base cuneate or rounded, infrequently truncate or somewhat cordate, predominantly more or less conspicuously hastate in Florida and adjacent territory; Appalachian Mountains eastward and southward to the Coast, westward roughly to the Ohio and lower Mississippi Valleys.

Leaves uniformly rounded or cuneate toward the base from above, or infrequently about, the middle, the margins essentially flat or somewhat revolute; distribution cited above, except Florida in general ..... ssp. *tuberosa*

Leaves predominantly with a more or less conspicuous hastate dilation toward the base, infrequently abruptly truncate, cordate, or essentially cuneate, the margins commonly more or less crisped; Florida and closely adjacent territory ..... ssp. *Rolfsii*

Leaves typically ovate to oblong-lanceolate, i. e. broadest below the middle, intergrading to oblong and elliptic, particularly eastward, the apex chiefly acuminate or narrowly acute, the base truncate or cordate, the margins flat or somewhat revolute; Arizona, southern Utah, and eastern Colorado to southern Minnesota and eastward to the Ohio and lower Mississippi Valleys ..... ssp. *interior*

I have accumulated a considerable mass of statistical data which I intend to publish elsewhere, and which I have no doubt will constitute a convincing proof of the genetic significance of the three subspecies. The category of subspecies has been employed because the data obtained indicate that when graphically presented the character scores will coincide satisfactorily with the "continuous stepped cline" distinguished by J. S. Huxley (Bijdr. Dierk. 27:491. 1939) for numerous subspecies of animals. Huxley's "clines" undoubtedly will be found valid, if not extensible, when that method is applied widely to plant populations. I should explain further that I have decided to follow a suggestion of Huxley (in 'The New Systematics', Oxford, 1940, p. 37) regarding the treatment of two or more intergrading populations: thus I have labelled intergrading specimens, particularly in the Ohio and lower Mississippi Valleys, as "*Asclepias tuberosa* cl. *tuberosa-interior*," the abbreviation denoting the word "cline." I consider that this form of label is convenient, approximates biological reality, and is far more satisfactory than arbitrarily to assign an intergrade either to *A. t. tuberosa* or to *A. t. interior*. This method doubtless may be used in the case of intergrading varieties as well.

(To be continued)

Explanation of Plate

PLATE 20

Asclepias tuberosa ssp. *tuberosa* and *A. tuberosa* ssp. *interior*. Explanation in the text.

WOODSON—SOME NORTH AMERICAN ASCLEPIADS

THE LILIACEOUS GENUS POLYGONATUM IN NORTH AMERICA[1]

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A cytotaxonomic study of the North American species of *Polygonatum* was begun by the writer in 1935 at the suggestion and under the direction of Dr. Edgar Anderson and Dr. J. M. Greenman. Most of the work was completed within the next three years. Publication was delayed, however, because there still remained several involved problems, and it was hoped that additional field study might provide answers to some unsettled questions. It now seems desirable, in view of recent publications on the group, to present the conclusions to date and to point out some of the problems yet to be solved.

History

The generic name *Polygonatum* is derived from the character of the rhizome and is explained by Miller[2] as follows:

> "so call'd of πολὺ *much*, and γονὺ a *Knee*, because it has many little Knees, for the Root is very knotty; It is also call'd *Solomon's-Seal*, because the Knots of the Root somewhat resemble a Seal."

The first use of the name *Polygonatum*, subsequent to the publication of Linnaeus's 'Species Plantarum' in 1753, was by Miller in the 'Abridgement' from 'The Gardener's Dictionary', published in 1754.[3] Linnaeus[4] listed three species of *Polygonatum* under the genus *Convallaria*, namely, *C. verticillata*, *C. Polygonatum* and *C. multiflora*. These were treated under the generic name *Polygonatum* by Allioni in 1785.[5] The specific epithet of *Convallaria Polygonatum*, however, was changed to *officinale*. Thus, in accordance with the International Rules of Botanical Nomenclature, the name of the type species *(Convallaria Polygonatum* L.*)* becomes *Polygonatum officinale* All.

The first American species mentioned in literature is *Convallaria biflora*, described by Walter[6] in 1788. In 1797, Poiret[7] described *C. hirta* Bosc, a species

[1] An investigation carried out at the Missouri Botanical Garden in the graduate laboratory of the Henry Shaw School of Botany of Washington University. A preliminary report was submitted as a thesis in partial fulfillment of the requirements for the degree of Master of Science.

[2] Miller, Philip. The Gardeners Dictionary, ed. 1. 1731.

[3] See Druce, G. Claridge. The abridgement of Miller's Gardener's Dictionary of 1754. Bot. Exch. Club & Soc. Brit. Isles Rept. 3:426-436. 1914, for a detailed account of this 'Abridgement', which seems to have escaped the notice of many botanical writers.

[4] Linnaeus, C. Species plantarum, ed. 1. 1:315. 1753.

[5] Allioni, Carlo. Flora pedemontana 1:130. 1785.

[6] Walter, Thomas. Flora caroliniana, p. 122. 1788.

[7] Poiret, J. L. M., in Lamarck, Encyclopédie méthodique. Botanique 4:369. 1797.

Issued November 30, 1944.

with hispid stems and pubescent leaves, said to have been sent from North America by Crevecoeur. However, no North American species with hispid stems is known to present-day botanists. In 1803, Michaux[8] united all of the American species with the European *C. multiflora*. Willdenow,[9] in 1806, described *C. pubescens* and *C. canaliculata* Mühl. In 1814, Pursh[10] transferred all these species to *Polygonatum*, but changed the name *biflora* of Walter to *angustifolium*. He also added the European *P. latifolium* to his list of North American species. Poiret,[11] in 1816, described *Convallaria parviflora*, another species of doubtful affinities. Schultes[12] added *C. commutata* in 1830, and Dietrich[13] proposed *Polygonatum giganteum* in 1835. In 1839, Hooker[14] referred all of his American specimens to *P. multiflorum β. Americanum*. Torrey,[15] in 1824, had recognized five species under *Convallaria*, but in 1843, he, too, referred them all to the European *P. multiflorum*.[16] Wood,[17, 18, 19] in the several editions of his 'Class-book of Botany' and in his 'American Botanist and Florist', considered the American species successively as varieties of *P. multiflorum* and of *P. biflorum*. In 1906, Greene[20] proposed three more species for the list, namely, *P. cuneatum*, *P. virginicum* and *P. boreale*. The New Mexican species was described by Wooton and Standley[21] as *Salomonia cobrensis* in 1913. Recent editions of Gray's 'Manual'[22] and Britton and Brown's 'Illustrated Flora'[23] recognize only two species, a pubescent one erroneously referred to as *P. biflorum*, and *P. commutatum* which includes the earlier *Convallaria biflora* of Walter.

More recent work on the genus has resulted in the description of numerous varieties and the making of various combinations. Farwell,[24] in 1915, reviewed the previous work on *Polygonatum*, divided the genus into two groups of species, the PUBESCENTES and the GLABRATA, and recognized in all five species and six varieties, several of which were proposed as new. In subsequent papers,[25, 26, 27] he

[8] Michaux, André. Flora boreali-americana 1:202. 1803.
[9] Willdenow, Karl Ludwig. Hortus berolinensis 1:45, *pl. 45*. 1806.
[10] Pursh, Frederick. Flora americae septentrionalis 1:234, 235. 1814.
[11] Poiret, J. L. M., in Lamarck, Encyclopédie méthodique. Botanique. Suppl. 4:29. 1816.
[12] Schultes, J. H., in Schultes & Schultes, Systema vegetabilium 7²:1669-1671. 1830.
[13] Dietrich, A., in Otto & Dietrich, Allgemeine Gartenzeitung 3:222, 223. 1835.
[14] Hooker, W. J. Flora boreali-americana 2:176. 1839.
[15] Torrey, John. A flora of the northern and middle sections of the United States, pp. 356, 357. 1824.
[16] Torrey, John. A flora of the state of New York 2:299. 1843.
[17] Wood, Alphonso. Class-book of botany, ed. 1, p. 396. 1845; ed. 2, p. 553. 1847.
[18] Wood, Alphonso. Class-book of botany; flora of the United States and Canada, p. 714. 1861.
[19] Wood, Alphonso. The American botanist and florist, p. 346. 1870.
[20] Greene, E. L. Leaflets of botanical observation and criticism 1:181, 182. 1906.
[21] Wooton, E. O., and P. C. Standley. Descriptions of new plants preliminary to a report upon the flora of New Mexico. Contrib. U. S. Nat. Herb. 16:109-196, *pl. 48-50*. 1913.
[22] Gray's New manual of botany, ed. 7. Revised by B. L. Robinson and M. L. Fernald, p. 292. 1908.
[23] Britton, N. L., and Addison Brown. An illustrated flora of the northern United States, Canada and the British possessions, ed. 2. 1:521. 1913.
[24] Farwell, O. A. Notes on the Michigan species of *Polygonatum*. Bull. Torr. Bot. Club 42:247-258, *pl. 12-18*. 1915.
[25] Farwell, O. A. Notes on the Michigan flora. Rept. Mich. Acad. Sci. 20:161-195. 1918.
[26] Farwell, O. A. Notes on the Michigan flora. III. Rept. Mich. Acad. Sci. 22:177-185. 1921.
[27] Farwell, O. A. Contributions to the botany of Michigan, No. 15. Am. Midl. Nat. 11:72-85. 1928.

has described *P. melleum*, presented several minor additions, and considerably modified his earlier concepts. Gates,[28] in 1917, revised the genus for North America, recognizing *P. pubescens*, *P. biflorum*, *P. commutatum*, *P. giganteum* and *P. cobrense*, as well as several varieties. *P. hirtum*, *P. canaliculatum* and *P. parviflorum* were included as doubtful or unidentified species. In 1927, Bush[29] accepted twelve North American species.

During the course of the present investigation, the writer has been able to examine many times the amount of herbarium material seen by any previous student of the problem. She has studied in the field all entities herein recognized with the exception of *P. biflorum* and *P. biflorum* var. *hebetifolium*, and at one time or another has had all of the entities except the latter under cultivation. From this abundant material it has been possible to establish the great variation which some of the biological species may exhibit, and to realize that many of the proposed segregates are nothing more than extreme individuals of no taxonomic importance. In the present treatment only four species, two of which are difficult if not impossible to separate completely on morphological grounds, and three varieties of one species are recognized. Only the North American species are discussed in this paper.

Morphology

The diagnostic characters separating species in *Polygonatum*, as in many other genera of the Liliaceae, may easily escape notice. They are inconspicuous and often are obscured by extreme variability in size and aspect of the plants.

Underground parts.—The genus is characterized by the presence of creeping knotted branching rhizomes. These have been observed to vary only in size, this variation being correlated with the general size of the whole plant. Deam[30] reports that the rhizomes grow near the surface in *P. pubescens* and deep in the ground in *P. biflorum* and *P. commutatum*. This difference appears to be related to differences in habit and habitat.

Stem.—A single upright stem rises from the rhizome each year (or one from each branch of the rhizome). In all North American species the stem is glabrous. It may be terete or ancipital, or sometimes somewhat grooved or channelled, but this character is not definite enough to have much value in species delimitation. The stem is almost strictly vertical to arching to such a degree that the upper part is horizontal. The amount of arching seems due, at least in part, to the size of the plant. The proportion of the leafy to the naked part of the stem seems to be a good character to aid in separating some of the species and varieties. In *P. biflorum* the leafy part is shorter than the lower naked part; in *P. biflorum* var. *melleum* the leafy and naked parts are about equal in length; in *P. biflorum*

[28] Gates, R. R. A revision of the genus *Polygonatum* in North America. Bull. Torr. Bot. Club 44:117-126, *pl. 4–6*. 1917.
[29] Bush, B. F. The species of *Polygonatum*. Am. Midl. Nat. 10:385-400. 1927.
[30] Deam, Charles C. Flora of Indiana, pp. 319, 320. 1940.

var. *necopinum* and *P. commutatum* the leafy part is usually considerably longer than the naked part.

Leaves.—Some of the best diagnostic characters are to be found in the leaves, both in their shape and in the texture and surface characters. In all the North American species the leaves are alternate. They are broadly oval, elliptic, ovate-lanceolate or nearly linear, the size and shape varying considerably within each of the species. In most cases the leaves are about 2 to 4 times as long as broad, but in *P. biflorum* var. *hebetifolium* they are very long and narrow, being 5 to 9 times as long as broad. In *P. pubescens* and *P. cobrense* the leaves are shortly petiolate; in *P. biflorum* var. *melleum* they vary from sessile to shortly petiolate; in the others they are sessile. The nervation of the leaves presents a nearly constant character which can quite easily be used in the separation of entities. The leaves of *P. pubescens*, *P. biflorum* and vars. *hebetifolium* and *necopinum*, and *P. cobrense* have few major nerves, only the midrib being prominent for the full length of the leaf. The leaves of *P. biflorum* var. *melleum* and *P. commutatum* are many-nerved. In *P. biflorum* var. *melleum* the nerves are all nearly equal in size, prominent in the lower half of the leaf and gradually fading out above the middle of the leaf. In *P. commutatum* the many strong nerves are prominent the full length of the leaf, with the midrib somewhat larger than the rest. *P. pubescens* is easily separated from the other species by the pubescence on the lower surface of the leaves. The hairs are whitish, short, straight and regular. They are found on the minor longitudinal nerves, less frequently on the more prominent nerves. All other species have completely glabrous leaves.

The lowest leaf is a cauline bract, usually set on the stem at a sharper angle than the other leaves. In *P. pubescens* and *P. cobrense* this bract is papery and caducous. In *P. biflorum* and its varieties and in *P. commutatum* it is leaf-like, green and persistent.

Inflorescence.—In most of the species each axillary peduncle bears 1 or 2, or rarely 3, flowers. In *P. biflorum* var. *melleum* the number varies from 2 to 4. In *P. commutatum* there is great variation in the inflorescence, both in the number of flowers (1 to 15) and in the relative lengths of pedicels and peduncle; also the pedicels in one inflorescence are sometimes equal and sometimes very unequal. In *P. biflorum* var. *hebetifolium* the peduncles are very long and slender. Those in *P. pubescens* and *P. cobrense* are strongly and sharply deflexed.

Differences in the position of the lowest peduncle in *P. pubescens*, *P. biflorum* and *P. commutatum*, as pointed out by Deam in his 'Flora of Indiana', have been emphasized by Fernald,[31] who reports that of the specimens examined by him the lowest peduncle was from the second axil in 66 per cent of the plants of *P. pubescens*, from the third axil in 59 per cent of those of *P. biflorum*, and from the fourth or fifth axil in 72 per cent of those of *P. commutatum*. These figures,

[31] Fernald, M. L. Specific distinctions between *Polygonatum biflorum* and *P. canaliculatum*. Rhodora 46:9-12. 1944.

however, lose some of their significance when it is remembered that the first green "leaf" in *P. biflorum* and *P. commutatum* is actually a cauline bract, and that there is possibility for considerable error in separating these two species on morphological criteria alone.

Perianth.—The size and color of the perianth are of some value in distinguishing species. *P. pubescens* has the smallest flowers, usually 10 or 11 mm. long. The flowers of *P. biflorum* var. *melleum* are also quite small, 12 to 15 mm. long. The other species and varieties have larger flowers, up to 23 mm. long in *P. cobrense*, *P. biflorum* var. *hebetifolium* and *P. commutatum*. In *P. biflorum* var. *hebetifolium* and *P. cobrense* the flowers are larger in proportion to the size of the whole plant than in any other North American species. The flowers are yellowish green in *P. pubescens*, whitish in *P. biflorum* and var. *necopinum*, yellowish in *P. biflorum* var. *melleum* and *P. biflorum* var. *hebetifolium*, and greenish white tipped with darker green in *P. commutatum*. Flower shape may be a good distinguishing character for living plants, but it cannot always be used with entire success on herbarium material. The flowers of *P. pubescens* are broadest below the middle of the perianth tube; the tube is contracted at the base of the perianth lobes, and the lobes are somewhat spreading. The flowers of the other species are nearly cylindric, being broadest at about the middle of the tube; the tube is not contracted at the base of the lobes, and the lobes are scarcely spreading.

Stamens.—The six stamens are inserted on the perianth tube, near the top of the tube in *P. pubescens*, at about the middle in the other species. The filaments of all species may be more or less papillose; they are densely so in *P. pubescens* and sometimes in *P. biflorum* var. *melleum*. In *P. biflorum* and its other varieties and in *P. cobrense* they are usually only slightly papillose. Those of *P. commutatum* vary from densely papillose to entirely smooth. The anthers are introrse.

Pistil.—The ovary is sessile to subsessile, oblong to globose, trilocular, with ovules several to a cell. The style is filiform, shorter than the perianth. The stigma is obtuse or capitate, and obscurely 3-lobed.

Fruit and seeds.—The fruit is a dark blue or black, globose, pulpy, several-seeded berry. The berries are usually larger and have more seeds in the larger *P. commutatum* than in the smaller plants of other species. The seeds are globose to more or less compressed, smooth, pale to brownish, with a stony endosperm.

Cytology

At the time the present study was undertaken very little was known of the cytology of the American species of *Polygonatum*. Incidental to other studies Cardiff[32] had reported a haploid chromosome number of 7 or 8 in material identified as *Salomonia biflora*. His figure of a meiotic metaphase in this species shows 7 bivalents. In 1933, Cartledge[33] reported a haploid number of 10 in *P. biflorum*

[32] Cardiff, Ira D. A study of synapsis and reduction. Bull. Torr. Bot. Club 33:271-303, *pl. 12–15*. 1906.

[33] Cartledge, J. L. Chromosomes of *Polygonatum*. Proc. Pennsylvania Acad. Sci. 7:78, 79. 1933.

and *P. commutatum*. Because of inaccuracies in the existing manuals of the region, it is likely that the former report should be referred to *P. pubescens* and the latter to *P. biflorum*. Chromosome studies on most of the species and varieties recognized in the present treatment were made by the writer independently of and several years in advance of the appearance of Eigsti's comprehensive cytological survey of the eastern North American species.[84] Eigsti reported chromosome counts on 19 collections of *Polygonatum* including *P. pubescens*, *P. biflorum*

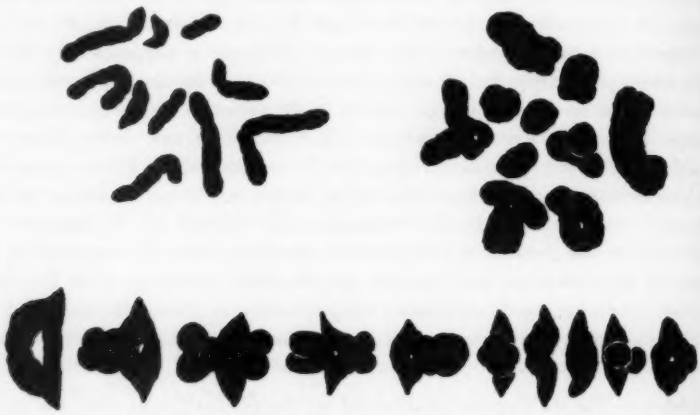

Fig. 1. Chromosomes of *Polygonatum cobrense*. Drawn from *Ownbey & Ownbey 1643*, from Canyon of Sapillo Creek, Gila National Forest, Grant Co., New Mexico. *Upper Left:* Metaphase of first pollen grain mitosis, n = 10. *Upper Right:* First meiotic metaphase in pollen mother cell, showing ten bivalents in polar view. *Below:* Individual bivalents from a single cell, drawn separately in side view. Magnification X 1800.

and *P. commutatum* (the last reported as *P. canaliculatum*). His counts and localities are listed in table 1 along with the writer's counts on these same and other species and varieties from eleven additional localities. Eigsti's counts were determined from colchicine-treated pollen tube mitoses. His technique appears to give a much better preparation than the aceto-carmine smear technique used by the writer to study the chromosomes at meiosis and pollen grain mitosis. This is particularly true in tetraploid material where it was not always possible for her to be sure that the chromosome number is exactly twenty.

From the table it is evident that the haploid chromosome number in all North American species of *Polygonatum* studied in recent years is either 10 or 20. *P. pubescens*, *P. cobrense* and *P. biflorum* with varieties *melleum* and *necopinum* are diploid, n = 10. All tetraploid (n = 20) specimens studied thus far belong to *P. commutatum*.

Meiosis is regular in all diploid species studied, with the formation of 10 bivalents on the metaphase plate. In the tetraploid *P. commutatum*, however,

[84] Eigsti, O. J. A cytological investigation of *Polygonatum* using the colchicine-pollen tube technique. Am. Journ. Bot. 29:626-636. 1942.

TABLE I

SUMMARY OF RECENT CHROMOSOME COUNTS ON THE NORTH AMERICAN SPECIES OF POLYGONATUM

Species	Locality	Collector	Chromosome Number	Investigator and Date
P. pubescens	Strafford Co., N. H.	A. R. Hodgdon	n=10	Eigsti '40
*P. pubescens**	Tolland Co., Conn.	G. S. Torrey	n=10	Eigsti '41
P. pubescens	Franklin Co., Ohio	Clyde Jones	n=10	Eigsti '41
P. pubescens	Davidson Co., Tenn.	A. J. Sharp	n=10	Eigsti '41
P. pubescens	Washtenaw Co., Mich.	J. T. Baldwin, Jr.	n=10	Eigsti '40, '41
P. pubescens	Baraga Co., Mich.	Edgar Anderson	n=10	R. Ownbey '39
P. pubescens	Oneida Co., Wisc.	Ruth E. Peck	n=10	R. Peck '37
P. pubescens	Wabasha Co., Minn.	C. O. Rosendahl	n=10	Eigsti '41
P. cobrense	Grant Co., N. Mex.	M. Ownbey & R. Ownbey	n=10	Ownbey & Ownbey '42, '44
P. biflorum	Middlesex Co., N. J.	M. A. Chrysler	n=10	Eigsti '41
P. biflorum	Prince Georges Co., Md.	Ronald Bamford	n=10	Eigsti '41
P. biflorum	Leon Co., Fla.	H. Kurz	n=10	R. Ownbey '38, '39
P. biflorum var. *melleum*	St. Clair Co., Mich.	Edgar Anderson & R. Peck	n=10	R. Ownbey '38
P. biflorum var. *necopinum*	Pennington Co., S. Dak.	M. Ownbey & R. Ownbey	n=10	R. Ownbey '39
P. commutatum†	Floyd Co., Va.	J. T. Baldwin, Jr.	n=20	Eigsti '39, '40, '41
P. commutatum	Wythe Co., Va.	Edgar Anderson & Wm. Brown	n=20	R. Ownbey '39
P. commutatum†	Durham Co., N. C.	L. E. Anderson	n=20	Eigsti '40
P. commutatum†	Washtenaw Co., Mich.	J. T. Baldwin, Jr.	n=20	Eigsti '41
P. commutatum†	Elkhart Co., Ind.	O. J. Eigsti	n=20	Eigsti '41
P. commutatum†	Hennepin Co., Minn.	C. O. Rosendahl	n=20	Eigsti '41
P. commutatum†	Hennepin Co., Minn.	C. O. Rosendahl	n=20	Eigsti '41
P. commutatum†	Johnson Co., Iowa	W. A. Anderson	n=20	Eigsti '41
P. commutatum†	Monona Co., Iowa	George Goodman	n=20	Eigsti '41
P. commutatum	St. Louis Co., Mo.	Maude Lodewyks & R. Peck	n=20±	R. Peck '36
P. commutatum	St. Louis Co., Mo.	M. Ownbey	n=20±	R. Ownbey '38
P. commutatum†	Cole Co., Mo.	Mrs. H. H. Leake	n=20	Eigsti '41
P. commutatum	Butler Co., Mo.	Edgar Anderson	n=20±	R. Ownbey '38
P. commutatum	Caddo Parish, La.	Mrs. James L. Dorman	n=20±	R. Ownbey '39
P. commutatum†	Cleveland Co., Okla.	O. J. Eigsti	n=20	Eigsti '39, '40, '41
P. commutatum†	Cleveland Co., Okla.	O. J. Eigsti	n=20	Eigsti '40, '41

*Described as pubescent, and diploid, but listed as *P. canaliculatum*—obviously a mistake.

†Reported as *P. canaliculatum*, a name now considered to be synonymous with *P. biflorum* and unavailable, therefore, for the tetraploid species.

there appears to be always some multivalent formation. This may result in unequal distribution of the chromosomes to the daughter nuclei, possibly accounting for seeming variation from the expected 20 chromosomes at mitosis in the pollen grains. Such irregularities are much more likely to be evident at this division than later at the pollen tube mitosis studied by Eigsti.

No karyotypic differences between the species other than tetraploidy are reported by Eigsti. In all of the diploid species studied there are 6 long and 4 short chromosomes; 12 long and 8 short, in the tetraploid. Eigsti states that in the diploid species 6 chromosomes have sub-terminal and 4 have sub-median insertions; in the tetraploid, 12 chromosomes have sub-terminal, 8 have sub-median insertions. An examination of his photographs, however, reveals that in one-third of his collections of *P. pubescens* and in all of his collections of *P. biflorum* there are 5 chromosomes with sub-median and 5 with sub-terminal constrictions. This latter condition agrees with the writer's observations in *P. biflorum* var. *melleum* and *P. biflorum* var. *necopinum*. The chromosomes of *P. cobrense* are shown in fig. 1.

Stomata size and distribution have recently been suggested and found useful in certain groups of plants as a means of detecting polyploidy through the use of herbarium specimens.[35, 36, 37] Sax and Sax found, in the genera which they investigated, that stomata frequency was a better index to polyploidy than stomata length. Babcock and Stebbins use stomata length. In *Polygonatum* also, stomata length is of more value. The chromosome numbers of the diploid *P. biflorum* and the tetraploid *P. commutatum* are correlated with either stomata measurement. In general, the stomata of *P. biflorum* are shorter and more frequent than those of *P. commutatum*, but there is considerable overlapping in the size and distribution ranges. In the diploid *P. pubescens*, the size of the stomata is similar to that in *P. biflorum*, but the frequency is like that in *P. commutatum*. The diploid *P. biflorum* var. *melleum* has very short stomata. On the other hand, *P. cobrense*, also diploid, and *P. biflorum* var. *hebetifolium*, whose chromosome number is unknown but whose morphology suggests that it is diploid, have stomata as long as the longest found in the tetraploid. Thus it is apparent that, although stomata size is of some use in separating the closely related diploid *P. biflorum* and tetraploid *P. commutatum*, it cannot be relied upon, in the genus as a whole, as a method of detecting polyploids.

In the species investigated, a much stronger correlation was found between stomata size and flower length than between stomata size and chromosome number. The flowers of *P. biflorum*, like the stomata, are usually but not always shorter than those of *P. commutatum*. *P. pubescens* and *P. biflorum* var. *melleum* have short flowers and stomata; *P. cobrense* and *P. biflorum* var. *hebetifolium* have very long flowers and stomata.

[35] Sax, K., and H. J. Sax. Stomata size and distribution in diploid and polyploid plants. Journ. Arnold Arboretum 18:164-172, *pl. 205*. 1937.

[36] Babcock, E. B., and G. L. Stebbins, Jr. The American species of *Crepis*, their interrelationships and distribution as affected by polyploidy and apomixis. Carnegie Inst. Wash. Publ. No. 504. 1938.

[37] Stebbins, G. L., Jr. Notes on some systematic relationships in the genus *Paeonia*. Univ. California Publ. Bot. 19:245-266. 1939.

Distribution

Polygonatum is widely distributed in north temperate regions. There are many more species in Europe and in temperate Asia than in North America, but these have not been studied in this investigation. In North America, the genus is found from the Atlantic Ocean to the Black Hills of South Dakota, and from southern Canada to northeastern Mexico. One species, *P. cobrense*, occurs in a restricted area in southwestern New Mexico and eastern Arizona.

Generic Relationship

The two genera perhaps most closely related to *Polygonatum* are *Streptopus* and *Disporum*, both with extensive north temperate ranges. Baker[38] included *Polygonatum* with *Convallaria* and other genera in the tribe Convallarieae of the Asparagaceae. What is perhaps a better way to treat the genus is that found in Bentham and Hooker's 'Genera Plantarum',[39] where it is included with *Streptopus*, *Disporum*, *Smilacina*, *Maianthemum*, etc., in the tribe Polygonateae of the Liliaceae, and in Engler and Prantl's 'Natürlichen Pflanzenfamilien',[40] where it is placed with *Clintonia*, *Tovaria* [*Smilacina*], *Majanthemum*, *Disporum*, *Streptopus*, etc., in the Asparagoideae-Polygonateae of the Liliaceae.

Acknowledgments

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Abbreviations

The herbaria from which loans of material for study have been obtained and from which citations are made in this treatment are indicated by the following abbreviations:

C—Herbarium of the National Museum of Canada.
D—Personal Herbarium of Charles C. Deam.
Farwell—Personal Herbarium of O. A. Farwell.
FM—Herbarium of the Chicago Museum of Natural History (Field Museum).
G—Gray Herbarium of Harvard University.

[38] Baker, J. G. Revision of the genera and species of Asparagaceae. Journ. Linn. Soc. [Lond.] Bot. 14:508-632, *pl. 17–20*. 1875.
[39] Bentham, G., and J. D. Hooker. Genera Plantarum 3[2]:768, 769. 1883.
[40] Krause, K., in Engler & Prantl, Die natürlichen Pflanzenfamilien, 2. Aufl. 15a:368-370. 1930.

M—Herbarium of the Missouri Botanical Garden.
Minn—Herbarium of the University of Minnesota.
MS—Herbarium of the Michigan State College of Agriculture.
NY—Herbarium of the New York Botanical Garden.
NYCP—Herbarium of the New York College of Pharmacy.
RM—Rocky Mountain Herbarium of the University of Wyoming.
UF—Herbarium of the Agricultural Experiment Station, University of Florida.
UM—Herbarium of the University of Michigan.
US—United States National Herbarium.
WS—Herbarium of the State College of Washington.
WVU—Herbarium of West Virginia University.

Taxonomy

Polygonatum [Tourn.] Miller, Gard. Dict. Abridg., ed. 4. 1754, in part; Adans., Fam. **2**:54. 1763; All., Fl. Ped. **1**:130. 1785, in major part; Baker in Journ. Linn. Soc. [Lond.] Bot. **14**:552-561. 1875; Benth. & Hook., Gen. Pl. 3^2:768, 769. 1883; Krause in Engler & Prantl, Nat. Pflanzenf. 2. Aufl. **15a**:368-370. 1930.

Convallaria L., Gen. Pl., ed. 5, p. 148. 1754, in part.
Salomonia Heist. ex Fabricius, Enum. Pl. Hort. Helmstad., ed. 2, p. 38. 1763.
Evallaria Neck., Elem. 3:189. 1790.
Axillaria Rafin. in Journ. Phys. 89:261. 1819.
Siphyalis Rafin., Fl. Tellur. 4:17. 1836.
Campydorum Salisb., Gen. Pl. Fragm., p. 64. 1866.
Sigillum [Trag. ex] Montand., Guide Bot., p. 310. 1868.
Periballanthus Franch. & Sav., Enum. Pl. Jap. 2:524. 1879.

Perennial herbs with horizontal, creeping, knotted rhizomes and fibrous roots; stem erect or arching, unbranched, glabrous or pubescent (glabrous in all North American species), naked below, leafy above, with one or more papery sheathing bracts at the base; leaves alternate, opposite or verticillate (alternate in all North American species), amplexicaul, sessile, or shortly petiolate, broadly oval to ovate-lanceolate to linear, glabrous on both sides or with a fine pubescence on the veins below; inflorescence axillary, the solitary peduncles each bearing a single flower, or two or more jointed pedicels each bearing a flower; peduncles and pedicels glabrous or pubescent (glabrous in all North American species); floral bracts much reduced, subulate, caducous; flowers pendulous, with the calyx and corolla united into a cylindric tube, 6-lobed at the top; perianth lobes usually shorter than the tube, sometimes spreading in the mature flower, glandulose-barbate at the tip inside; stamens six, included, inserted on the perianth tube; filaments filiform or flattened, smooth to roughly papillose; anthers oblong-linear to sagittate, 2-lobed at the base, introrse; ovary sessile to subsessile, oblong to globose, 3-locular; style filiform, shorter than the perianth; stigma obtuse or capitate, obscurely 3-lobed; ovules several in a cell; fruit a dark blue or black, globose, pulpy, several-seeded berry; seeds globose to more or less compressed, smooth, pale to brownish, with stony endosperm.

Type Species: *Convallaria Polygonatum* L., Sp. Pl. **1**:315. 1753 (=**Polygonatum officinale** All., Fl. Ped. **1**:131. 1785).

Key to the Species and Varieties

a. Cauline bract papery, caducous; peduncles strongly and sharply deflexed.
  b. Leaves pubescent on the veins beneath; flowers small, 8 to 14 (usually 10 or 11) mm. long; perianth tube constricted at base of lobes, lobes spreading at anthesis; filaments inserted near the top of the tube; diploid (n = 10) ..... 1. *P. pubescens*
  bb. Leaves glabrous on both sides; flowers large, 17 to 23 mm. long; perianth tube cylindrical, not constricted, lobes erect at anthesis; filaments inserted near the middle of the tube; diploid (n = 10) ..... 2. *P. cobrense*

aa. Cauline bract green, leaf-like, persistent; peduncles arcuate, not strongly deflexed; plant entirely glabrous; flowers usually 12 to 23 mm. long; perianth tube cylindrical, not constricted, lobes scarcely spreading; filaments inserted near the middle of the tube.
  c. Chromosome complement diploid (n = 10);* plants dainty, usually less than 6 dm. high; peduncles 1- or 2 (to 4)-flowered; leaves with only the mid-vein prominent for the full length.
    d. Upper leafy portion of the stem usually shorter than lower naked portion; leaves elliptic-lanceolate, few-nerved; peduncles 1- or 2-flowered; flowers 11 to 19 (usually 13 to 15) mm. long; widespread in eastern United States ..... 3. *P. biflorum*
    dd. Upper leafy portion of the stem about equalling lower naked portion in length; leaves variable in shape, elliptic-lanceolate to broadly elliptic, many-nerved; peduncles 2- to 4-flowered; flowers 12 to 15 mm. long; Michigan and Ontario, in the vicinity of Lake St. Clair ..... 3a. *P. biflorum* var. *melleum*
    ddd. Upper leafy portion of the stem about equalling lower naked portion in length; leaves oblong-lanceolate, 5 to 9 times as long as broad, few-nerved; peduncles 1- or 2-flowered; flowers large, 20 to 23 mm. long; along the Apalachicola River, western Florida ..... 3b. *P. biflorum* var. *behetifolium*
    dddd. Upper leafy portion of the stem longer than lower naked portion; leaves elliptic-lanceolate, few-nerved; peduncles 2-flowered; flowers 15 to 17 mm. long; Black Hills of South Dakota ..... 3c. *P. biflorum* var. *necopinum*
  cc. Chromosome complement tetraploid (n = 20); plants generally coarser, more robust, usually more than 6 dm. high, often much larger; peduncles 1- to 15 (usually 3 or more)-flowered; leaves with numerous veins prominent the full length; upper leafy portion of the stem usually longer than the lower naked portion ..... 4. *P. commutatum*

* Chromosome number given at the beginning of the paragraph here because it is the best character separating *P. biflorum* and *P. commutatum*; in other places it is supplementary information.

1. Polygonatum pubescens (Willdenow) Pursh, Fl. Am. Sept. 1:234. 1814.

Convallaria pubescens Willdenow, Hort. Berol. 1:45, *pl. 45*. 1806.[41]
Polygonatum multiflorum β. *pubescens* Wood, Class-book of Bot., ed. 1, p. 396. 1845.
Polygonatum multiflorum β. *americanum* Hooker, Fl. Bor. Am. 2:176. 1839 (apparently typical part).
Polygonatum biflorum sensu A. Gray, Manual, ed. 2, p. 466. 1856, and subsequent editions, not *P. biflorum* (Walter) Elliott, Sketch Bot. S. C. & Ga. 1:393. 1817.
Polygonatum multiflorum δ. *latifolium* Wood, Class-book of Bot. Fl. U. S. & Can., p. 714. 1861.
Polygonatum biflorum γ. *latifolium* Wood, Am. Bot. & Flor., p. 346. 1870.
Polygonatum cuneatum Greene, Leaflets 1:181. 1906.
Polygonatum pubescens var. *cuneatum* Farwell in Bull. Torr. Bot. Club 42:253, *pl. 13, B*. 1915; Am. Midl. Nat. 11:77. 1928.

[41] Synonyms are cited chronologically according to type.

Polygonatum pubescens f. *cuneatum* Victorin in Contrib. Lab. Bot. Univ. Montreal 14:28. 1929.

Polygonatum boreale Greene, Leaflets 1:181. 1906.

Polygonatum pubescens var. *boreale* Farwell in Am. Midl. Nat. 11:76. 1928.

Polygonatum boreale var. *australe* Farwell in Bull. Torr. Bot. Club 42:254, *pl. 14, B.* 1915.

Polygonatum pubescens australe Gates in Bull. Torr. Bot. Club 44:119, *pl. 4, A.* 1917.

Polygonatum pubescens var. *boreale* subvar. *australe* Farwell in Am. Midl. Nat. 11:77. 1928.

Polygonatum boreale var. *multiflorum* Farwell in Rept. Mich. Acad. Sci. 20:170. 1918.

Polygonatum Farwellii Bush in Am. Midl. Nat. 10:390. 1927.

Polygonatum pubescens var. *multiflorum* Farwell in Am. Midl. Nat. 11:77. 1928.

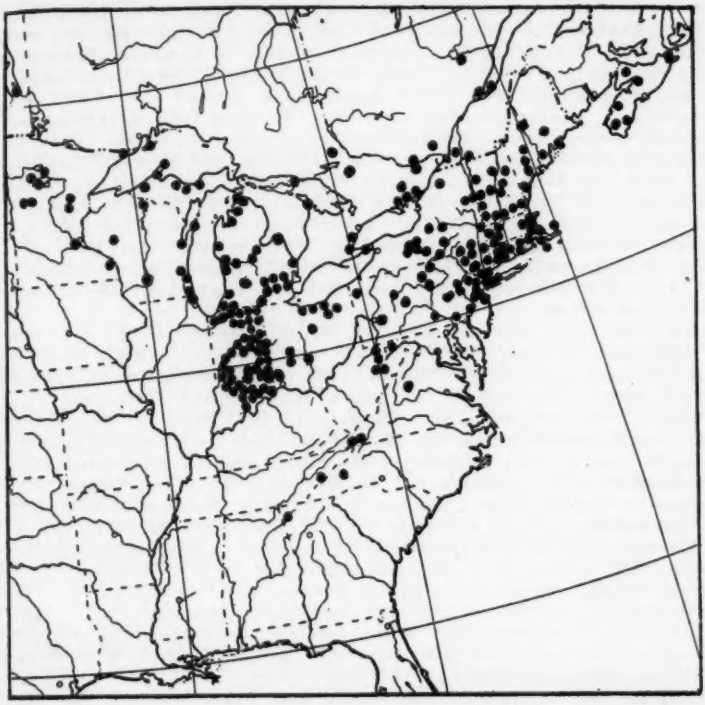
Polygonatum pubescens f. *fultius* Fernald & Harris in Rhodora 35:404, *fig. 1.* 1933.

Perennial herb, usually 3 to 6, but occasionally as much as 9 dm. high; rhizome slender; stem slender, erect or slightly arched at top, upper leafy portion of stem shorter than lower naked portion; leaves alternate, frequently secund, elliptic-lanceolate to elliptic or broadly oval, narrowed at the base to a short petiole, blade rounded to cuneate at the base, narrowed abruptly to an obtuse apex, 3.5 to 15 cm. long, 1 to 7 cm. broad, glabrous above, glaucous, often minutely papillose, and with a fine pubescence on the minor nerves beneath, prominent nerves 3 to 9; cauline bract subulate, papery, caducous; peduncles axillary, solitary, slender, glabrous, strongly and sharply deflexed, usually none from the axil of the lowest leaf, usually 1- or 2 (occasionally 3 to 5)-flowered; pedicels slender, glabrous, subequal, usually shorter than the peduncle; flowers yellowish green, smaller than in the other North American species; perianth 8 to 14 (usually 10 or 11) mm. long, 2.5 to 5 mm. broad in pressed material, contracted at the base of the perianth lobes, minutely papillose inside; lobes of the perianth spreading at anthesis, papillose inside; filaments densely papillose, inserted near the top of the perianth tube; berry dark blue, usually between 7 and 10 mm. in diameter.

This species is easily distinguished by its pubescent leaves, deflexed peduncles and small flowers, with the perianth tube contracted at the base of the spreading lobes and the stamens inserted near the top of the tube. The numerous varieties which have been proposed were based mostly on leaf shape and size alone, and appear to be mere phases of a continuous series. None appears to have a significant geographical distribution. The larger, more vigorous-looking plants may have peduncles with from 3 to 5 flowers.

Distribution: In usually moist, rich woods, Nova Scotia and New England, south along the Appalachian Mountains to northern Georgia, west to Indiana, Illinois, Wisconsin, Minnesota, and Manitoba (Map 1).

Nova Scotia. Guysborough co.: Boylston, June, 1890, *Hamilton* (C). Colchester co.: wooded banks, Truro, June 11, 1883, *Macoun* (C). Cumberland co.: dryish woods along Kennedy Brook, Springhill Junction, July 18, 1920, *Pease & Long 20756* (G). Lunenburg co.: Bridgewater, July 21, 1910, *Macoun* (C, FM). Annapolis co.: mixed woods, south slope of North Mt., n. of Middleton, July 21, 1920, *Long 20757* (C,



Map 1. Distribution of *Polygonatum pubescens*. Since the map was made, additional specimens from New Jersey, West Virginia and Ohio have been seen. Based on Goode *Base Map* No. 102. By permission of The University of Chicago Press.

G). DIGBY CO.: moist thickets and borders of woods, Hectanooga, July 31, 1920, *Long & Linder 20758* (G).

QUEBEC. LAKE ST. JOHN CO.: on boulders, margins of woods, vicinity of St. Jerome, Laurentide Mts., June 30, 1920, *Victorin 10016* (G). MONTMORENCY CO.: exposed rocks, Grosse Isle, 40 mi. below Quebec, Aug. 28, 1922, *Victorin 16004* (G, US). QUEBEC CO.: Montmorency Falls, June 28, 1905, *Macoun* (C). MISSISQUOI CO.: dry limestone ledge, Philipsburg, Aug. 10, 11, 1923, *Knowlton* (G); woods, limestone, Philipsburg, May 24, 1930, *Victorin & Germain 34161* (G). CHAMBLY (?) CO.: Montagne de Beloeil, June 1, 1920, *Victorin 11005* (G). TERREBONNE CO.: woods, Lac Tremelant, July 31, 1922, *Churchill* (G). HULL CO.: rich woods, Hull, May 27, June 10, 1905, *Harrington 2285* (C); Hull cemetery, June 3, 1911, *Macoun* (C).

ONTARIO. CARLETON CO.: woods, Ottawa, May 28, 1893, *Macoun* (C); Ottawa, Aug. 20, 1894, *Macoun* (G); woods, McKays Bush, Ottawa, Aug. 21, 1894, *Macoun* (C); Dows swamp, by Rideau River, above Billings Bridge, May 21, 1903, *Macoun* (C). LEEDS CO.: Jones Falls, May 26, 1891, *Fowler* (US). FRONTENAC CO.: Battersea, June 1, 1893, *Fowler* (M, MS); Sharbot Lake, July 16, 1898, *Fowler* (FM). HASTINGS CO.: rich woods, vicinity of Belleville, May 30, 1877, *Macoun* (C). PEEL CO.: woods, Snelgrove, June 3, 1898, *White* (C). WENTWORTH CO.: woods, West End Spring, Hamilton, 1892, *Dickson* (C). WELLAND CO.: Point Abino, Lake Erie, Aug. 28, 1896, *A.A.A.S.*

Excursion (NY). NIPISSING DIST.: Skunk Lake Portage, Timagami Provincial Forest, Aug. 25, 1932, *Krotkov 5231* (G); rich woods, Cache Lake, Algonquin Park, June 12, 1900, *Macoun* (C). MANITOULIN DIST.: crevices and talus of hornblend cliffs and ledges, Cloche Peninsula, June 29, 1934, *Fernald & Pease 3239* (G). BRUCE CO.: maple grove, Lake Ira, Bruce Peninsula, June 4, 1934, *Krotkov 8854* (G).

MANITOBA. DISTRICT NOT DETERMINED: Lake Winnipeg Valley, 1851, *Bourgeau* (G).

MAINE. PENOBSCOT CO.: Orono, June, 1895, *Keinstead 1020* (US). HANCOCK CO.: trail between Jordans Pond and Eagle Lake, Mt. Desert, June 28, 1889, *Redfield 16438* (M). KNOX CO.: Union, 1916, *Cole 271* (US); rich shaded woods, near Washington Pond, 3 mi. n. of Washington, Aug. 24, 1929, *Steyermark 881* (M). SOMERSET CO.: Kineo, Sept. 13, 1893, *Kennedy* (G). FRANKLIN CO.: damp woodland, South Chesterville, May 18, 1902, *Eaton* (G). OXFORD CO.: Hartford, May, 1885, *Parlin* (G); dry wooded banks, Buckfield, Aug., 1895, *Parlin* (Minn). CUMBERLAND CO.: North Gray, July 10, 1915, *Fellows 7109* (US). YORK CO.: thin woods, South Berwick, May 27, 1934, *Neal 97* (Minn).

NEW HAMPSHIRE. COOS CO.: Randolph, Sept. 2, 1903, *Moore 1465* (G). GRAFTON CO.: rich woods, Hanover, May, 1936, *Beetle 240* (WS), *1098* (RM); alluvial woods, North Woodstock, July 15, 1915, *Fernald 11647* (G); Hanover, May 25, 1883, *Hitchcock* (M, Minn). ROCKINGHAM CO.: wooded bank of pond, Derry, Aug. 25, 1917, *Batchelder* (NY). HILLSBORO CO.: rich damp woods, Wilton, May 16, 1929, *Beattie* (RM); wooded roadside, Mason, May 28, 1914, *Batchelder* (US); wooded roadside bank, Merrimack, June 2, 1920, *Batchelder* (M); wooded roadside, Peterborough, Sept. 13, 1927, *Batchelder* (M). CHESHIRE CO.: woods, Jaffrey, July, 1897, *Robinson 202* (G).

VERMONT. CALEDONIA CO.: Peacham, May 22, 1887, *Blanchard* (FM, M, NY, RM, US). ORANGE CO.: palisades, Fairlee, July 6, 1927, *Mathias 140* (M, NY). CHITTENDEN CO.: Charlotte, May 26, 1878, *Horsford* (FM); rich moist woods, Milton, May 22, 1936, *Knowlton* (D). ADDISON CO.: rich woods, Bristol, July 11, 1935, *Knowlton* (D). RUTLAND CO.: woods, edge of Scanlon swamp, Brandon, May 16, 1921, *Dutton* (FM, M). BENNINGTON CO.: East Dorset, July, 1867, *Ames* (UM); Manchester, July 7, 1898, *Day 173* (FM, G, US). WINDHAM CO.: Westminster, Aug. 26, 1848, *Holton* (FM); at edge of woods on top of moist cliff, Wardsboro, May 26, 1937, *Moldenke & Moldenke 9593* (NY); woods, Westminster, June 16, 1898, *Robinson 47* (G).

MASSACHUSETTS. ESSEX CO.: moist woods, Essex Lakes, Hamilton, May 26, 1870, *Morong* (NY); Beverly, Sept., 1892, *ex herb. Peabody* (G); Marblehead, June 5, 1900, *Piper* (WS). MIDDLESEX CO.: woods, Horn Pond Mt., Woburn, May 14, 1905, *Bartlett 70* (UM); Westford, *Fletcher* (G); Seavers Woods, near boundary between Newton and Weston, May, 1893, *ex herb. Gilbert* (G); Auburndale, May 23, 27, 1894, *ex herb. Gilbert* (G); fresh pond, Cambridge, *Gray* (G); Stony Brook, May 15, 1897, *Greenman 2288* (M); rich woods, Shirley, May 30, 1914, *Hunnewell & St. John 1608* (WS); damp woods, Melrose, May 30, 1876, *Morong* (M); Ashland, June 30, 1877, *ex herb. Morong* (NY); open woods along Estabrook road, vicinity of Concord, May 27, 1915, *Norton 195* (US); Arlington, May 22, 24, 1900, *Piper* (WS); South Framingham, May 14, 1890, *Sturtevant* (M); vicinity of Cambridge, May 30, 1891, *Underwood 2760* (NY). SUFFOLK CO.: near Boston, 1816, *Boott* (US); Oak Island, May 23, 1897, *Greenman 2284* (M); Revere, Aug. 28, 1882, *Perkins* (C). NORFOLK CO.: cleft in rock, Stoughton, May 13, 1909, *Blake* (US); Blue Hills, May 28, 1854, *ex herb. Boott* (G); Brookline, *ex herb. Faxon* (G); Wellesley, May 18, 1889, *ex herb. Harlow* (NY); Blue Hill, near entrance to Blue Hill Reservation, Milton, May 20, 1911, *Kennedy* (G); Milton, May 27, 1900, *Murdoch 471* (FM). PLYMOUTH CO.: Middleboro, June 20, 1902, *Murdoch 1134* (FM). BARNSTABLE CO.: Provincetown, May 22, 1907, *Greenman 3013* (M); Provincetown, Sept. 2-11, 1901, *Hollick* (NY). DUKES CO.: Chappaquiddick Island, Sept. 15, 1917, *Bicknell* (NY); damp woods, near brook, Menemsha, Chilmark, June 10, 1917, *Seymour 1154* (G, US); low ground, off North Road, Chilmark, June 10, 1917, *Seymour 1899* (G); woods, West Tisbury, June 8, 1917, *Seymour 1900* (G). BRISTOL CO.: Nonquit, May 29, 1889, *Sturtevant* (M). FRANKLIN CO.: Sugar Loaf, 1818, *ex herb. Cooley* (MS); Sunderland, May 25, 1880, *Minott* (US); cool rich woods, Monroe Bridge, Mon-

roe, May 15, 1915, *St. John & Hill 11999* (WS); Ashfield, Aug. 8, 1909, *Williams* (G). HAMPSHIRE CO.: Amherst, May, 1890, *Morris* (Minn); roadside banks in wooded country, Huntington, Aug. 17, 1912, *Robinson 485* (G). HAMPDEN CO.: Russell, May 31, 1873, *Rusby* (UM); shaded brookside, Russell, May 17, 1913, *St. John & White 90* (WS). BERKSHIRE CO.: hedgerow, Adams, Aug. 27, 1901, *Day 101* (G); steep rocky wooded slope, North Adams, June 23, 1913, *Fernald & Long 9248* (G).

RHODE ISLAND. PROVIDENCE CO.: Cat Swamp, Providence, May 24, 1900, *Chamberlain 86* (US); woods, Providence, June, 1866, *Thurber* (G); Lonsdale, May 15, 1904, *Williams* (G).

CONNECTICUT. WINDHAM CO.: dry, but rich, woods and thickets, Thompson, May 17, 1918, *Weatherby 4224* (US). NEW LONDON CO.: damp rocky woods, Center Groton, Groton, May 28, 1933, *Jansson* (RM); Greeneville, June 3, 1885, *Lumsden* (C). MIDDLESEX CO.: Middletown, June, 1830, *Buckley* (M). HARTFORD CO.: fence rows, Southington, June 29, 1898, *Andrews 348* (G); hedges and fence rows, Southington, May 30, 1898, *Andrews 349* (G); woods, Southington, May 7, 1897, *Bissell 209–2659* (M); Glastonbury, May 28, 1932, *Denslow* (NY); Wethersfield, June, July, 1875, *Wright* (G); Farmington, June 4, 1884, *Wright* (M). NEW HAVEN CO.: New Haven, May 20, 1884, *Safford 42* (US). LITCHFIELD CO.: wooded trap-rocks, Woodbury, June 14, 1933, *Eames 11546* (G). FAIRFIELD CO.: Fairfield, May 17, 1895, *Eames* (US); edge of rich woods, Fairfield, May 17, 1896, *Eames 1* (G); Easton, May 10, 1905, *Eames & Godfrey 69* (UF); Redding, June 28, 1905, *Godfrey* (UF); vicinity of Greens Farms, July 5, 1894, *Pollard 144* (US).

NEW YORK. WARREN CO.: sandy roadside woods, w. of Odels, w. of Lake Sunnyside, n. of Glens Falls, Aug. 24, 1916, *Burnham* (G). WASHINGTON CO.: gravelly sandy woods, near Tripoli Cemetery, southern West Fort Ann, May 31, 1915, *Burnham* (G); road, Podunk to Wiggins mine, West Fort Ann, June 8, 1917, *Burnham* (G). RENSSELAER CO.: Troy, 1828, 1834, *Hall* (FM). COLUMBIA CO.: near Turedy Lake, May 30, 1926, *Beale & party* (NY); woods, Copake Falls, Aug. 28, 29, 1914, *Britton, Taylor & Stetson* (NY). GREENE CO.: Windham, July 28-31, 1909, *Taylor 864* (NY); Onteora, vicinity of Tannersville, July 2, 20, 1891, *Vail* (NY). DELAWARE CO.: Arkville, May 29-31, 1915, *Mulford & Wilson* (NY). DUTCHESS CO.: rich woods, vicinity of Clove, Sept. 7, 1915, *Standley & Bollman 12389* (US). ULSTER CO.: Panther Mt., Aug. 14, 1919, *Denslow* (NY); Shandaken, Aug. 30, 1919, *Denslow* (NY). SULLIVAN CO.: woods, near Wurtsboro, June, 1873, *Eggert* (M). ORANGE CO.: Southfields, Tuxedo, May 10, 1922, *Denslow* (NY); Otisville, Aug. 30, 1922, *Denslow* (NY); Goshen, Aug. 31, 1922, *Denslow* (NY); woodland, Highland Falls, May 23, 1915, *Pennell 2395* (NY). WESTCHESTER CO.: woods, Bronxdale, May 7, 1902, *Burnham 835* (G); Mount Pleasant, May 15, 1922, *Denslow* (NY); North Castle, May 23, 1923, *Denslow* (NY); vicinity of New Rochelle, 1908, *Garvens* (FM); woodland, North Tarrytown, May 9, 1915, *Pennell 2376* (NY). ROCKLAND CO.: Haverstraw, May 19, 1921, *Denslow* (NY); Ramapo, May 24, 1922, *Denslow* (NY); rocky woodland, Snedens Landing, Nov. 3, 1914, *Pennell 2334* (NY). BRONX CO.: Van Cortlandt Park, Caryl, Yonkers, May 11, 1893, *Bicknell 552* (NY); McLeans Woods, Bronx, May 13, 1913, *Holtzoff* (NY); Van Cortlandt Park, New York City, Apr. 29, 1921, *House 7726* (C); Bronx Park, New York City, May 11, 1896, *Nash 86* (NY). NEW YORK CO.: New York City, May 25, 1893, *ex herb. Curtis* (Minn); 54th St., New York City, May, 1848, *Leggett* (NY). SUFFOLK CO.: hilly rich woods, Cold Spring Harbor, May 23, 1928, *Ferguson 6529* (NY). NASSAU CO.: Roslyn, Sept. 12, 1919, *Ferguson* (NY); hilly rich woods, n. w. of Platsdale, July 17, 1926, *Ferguson 4160* (NY); hilly wet rich woods, Millneck, May 25, 1926, *Ferguson 4807* (NY). QUEENS CO.: Richmond Hill, May 11, 1904, *Bicknell* (NY); North Beach, May 16, 1927, *Ferguson 5410* (NY). ST. LAWRENCE CO.: rich woods, Canton, May 23, 1915, *Phelps 1384* (C, G, NY, US). ONEIDA CO.: ravine sides and rich woods, Utica, May 16, 1902, *Haberer 923* (G). ONONDAGA CO.: swamp, e. of Syracuse, *Bell* (US); near Syracuse, 1891, *Straub* (US). CHENANGO CO.: Bainbridge, Aug. 13, 1932, *Denslow* (NY). BROOME CO.: Binghamton, 1895, *Clute* (NY); rich woods, South Mt., Binghamton, *Millspaugh 885* (FM). TOMPKINS CO.: leaf-mold on ledges, north side of

Fall Creek Ravine, above Beebe Lake, Ithaca, May 17, 1915, *Eames 3737* (G, Minn); woods, Fall Creek Ravine and vicinity, north shore of Beebe Lake, Ithaca, May 27, 1915, *Eames 3744* (FM, G); rich woods, n. w. of Enfield Falls, Enfield, June 11, 1917, *Gerstboy 7884* (G); ravines, Ithaca, May, 1903, *Kauffman* (UM); flats near Lick Brook, Ithaca, May 23, 1920, *Muenscher & Bechtel 113* (WS); Six-mile Creek, Ithaca, May 26, 1883, *Pearce* (US). YATES CO.: without exact locality, *Sartwell* (FM). ONTARIO CO.: open woods, east side of Hemlock Lake, Canadice, May 18, 1915, *Thomas 3743* (G); moist woods, Geneva, June 4, 1882, *Wing* (M). LIVINGSTON CO.: glen, west side of Hemlock Lake, Conesus, May 20, 1915, *Thomas 3738* (G, M). COUNTY NOT DETERMINED: South Meadow, Adirondacks, Sept. 16, 1892, *ex herb. Clarke* (NY); Balsam Lake, Catskills, July, 1886, *Van Brunt* (NY).

NEW JERSEY. SUSSEX CO.: rich woods, Andover Junction, May 30, 1917, *Mackenzie 7642* (NY); wooded hillside, Sucker Pond, May 29, 1920, *Mackenzie* (NY); Franklin, Aug., 1879, *Rusby* (UM); woods, Hamburg, June 1, 1892, *ex herb. Van Sickle* (US). PASSAIC CO.: Butler, Sept. 22, 1922, May 14, 1923, *Denslow* (NY); woodlands, Greenwood Lake, May 19, 1907, *Mackenzie 2574* (M). BERGEN CO.: Fort Lee, May, 1898, *Wooton* (US). UNION CO.: Summit, July 30, 1868, *Leggett* (NY). SOMERSET CO.: Chimney Rock, May 21, 1932, *Drushel 7905* (M); dark moist woods along brook, Watchung, May 10, 1931, *Moldenke 1512* (NY). MIDDLESEX CO.: woodlands, Metuchen, May 18, 1919, *Mackenzie* (NY). MONMOUTH CO.: thickets, Cream Ridge, May 29, 1922, *Dreisbach 939* (FM); rich bottom woods, Freehold, Aug., 1917, *Mackenzie 7926* (NY); shaded marl slopes, Marlboro, Sept., 1917, *Mackenzie 8088* (NY); wooded marl banks, Marlboro, May 3, 1919, *Mackenzie* (NY). BURLINGTON CO.: wooded terraces along tributary, Rancocas Creek, 1 mi. n. e. of Pemberton, May 15, 1917, *Long* (WVU).

PENNSYLVANIA. BRADFORD CO.: woods, Athens, May 27, 1900, *Barbour 870* (RM). TIOGA CO.: Blossburg, Sept. 24, 1928, *Eggleston & Kelly 22766* (M, US). LYCOMING CO.: Deer Hole Mt., South Williamsport to summit, Sept. 21, 1928, *Eggleston & Kelly 22754* (US). MONROE CO.: Pocono Plateau, July, Aug., 1904, *Harshberger* (FM, G, M, RM, US). NORTHAMPTON CO.: Easton, July 14, 1896, *Tyler* (NY). SCHUYLKILL CO.: Uhls Mill, Spring Mountain, May 2, 12, 1906, *Williamson* (NY). DELAWARE CO.: rocky woods, Rockdale, Sept. 6, 1914, *Pennell 1658* (NY); rich woods, Wawa, May 3, 1915, *Pennell 2368* (NY). LANCASTER CO.: Mountville, May, 1889, *Eby* (M); Cedar Hill, 3 mi. n. of Lancaster, Apr. 24, 1889, *Small* (FM). CUMBERLAND CO.: near Eberlys Mill, May 4, 1888, *Small* (FM). CLEARFIELD CO.: dry rich woods, 2 mi. n. w. of Du Bois, May 18, 1941, *Wahl 947* (WS). BLAIR CO.: Bellwood, May 18, 1904, *Jennings* (M photo). WESTMORELAND CO.: woodlands, hillside, Chestnut Ridge, May 19, 1935, *Bright 12426* (Minn); ravine, North Trafford, May 29, 1937, *Emig* (M). CRAWFORD CO.: Hartstown, May 31, 1937, *Emig* (M); edge of woods, Hemlock Island, 5 mi. w. s. w. of Linesville, May 19, 1932, *Graham* (NY).

DELAWARE. COUNTY NOT DETERMINED: woodlands, June, 1865, *Canby* (NYCP).

MARYLAND. GARRETT CO.: without locality, July 24, 1878, *Smith* (US).

WEST VIRGINIA. BROOKE CO.: Franklin Community, Wellsburg, June 6, 1937, *Emig* (M). OHIO CO.: shaded hillside, Middle Wheeling Creek, 6 mi. from mouth, July, 1937, *Bartholomew 345* (WVU); Oglebay Park, May 4, 1929, *Strausbaugh 46* (WVU); Hickory Hill, Wheeling, May 11, 1937, *West 157* (WVU). MARSHALL CO.: bank of Fish Creek near mouth of Lower Bowman Run, June 15, 1940, *Bartholomew 148* (WVU). MONONGALIA CO.: Morgantown, May 12, 1924, *Bourne 45* (WVU); rich woods, Falling Run, Morgantown, May 2, 1890, *Millspaugh 75* (FM, NY, WVU); ½ mi. below Morgantown, May 16, 1937, *Myers* (WVU); Wadestown, *Thomas* (WVU). MARION CO.: College woods, May 9, 1937, *Beade* (WVU); near mouth of Pricketts Creek, May 16, 1937, *Harris* (WVU); rich shady moist woods, Rymer, May 15, 1937, *Thorn* (WVU). TAYLOR CO.: along Tygarts River, 2 mi. n. of Grafton, July 7, 1937, *Core 5501* (WVU). BARBOUR CO.: dry mixed woods, east bank of Tygart Valley River, near Tygart Junction, Sept. 24, 1904, *Moore 2564* (G, RM). UPSHUR CO.: Buckhannon, May 8, 1895, *Pollock* (M, US). PENDLETON CO.: 1 mi. n. of Mouth of Seneca, July 16, 1937, *Core 6150* (WVU); eastern spur of the main ridge of the Alleghany Mts., above Horton, Sept. 17, 1904, *Greenman 96* (G). RANDOLPH CO.: Pickens, Spring, 1938, *Perine* (WVU).

PLEASANTS CO.: near St. Marys, May 8, 1937, *Brooks & Margolin* (WVU). RITCHIE CO.: Mole Hill, Route 74, July 8, 1937, *Core 5611* (WVU); Cairo, Apr. 19, 1930, *Goodwin* (WVU). CALHOUN CO.: Pink, Apr. 22, 1933, *Harris* (WVU). KANAWHA CO.: rich shaded woods, around rock cliffs or old logs, Queen Shoals, Apr. 20, 1936, *Randolph 118* (WVU). CABELL CO.: near Lesage, May 1, 1937, *Brooks & Margolin* (WVU). FAYETTE CO.: near Glendale, May 1, 1937, *Brooks & Margolin* (WVU); Nuttallsburg, 1890, *Nuttall 46* (WVU). SUMMERS CO.: near Hinton, May 2, 1932, *Boone 60* (WVU); along stream, hollow of Hinton Mt., in horseshoe bend, May 4, 1939, *Tosh* (WVU). RALEIGH CO.: side of Baloff Mt., May 13, 1940, *Tosh 36* (WVU).

VIRGINIA. MADISON CO.: deep shade, s. and s. e. of Skyland, Shenandoah National Park, May 28, 1936, *Camp 1224* (NY). WYTHE CO.: shaded limestone bluffs, Wytheville, May 3, 1936, *Svenson 7767* (G). SMYTH CO.: Nicks Creek, vicinity of Marion, June 4, 1892, *Britton, Britton & Vail* (NY); Hungry Hollow, n. e. of Marion, May 24, 1892, *Small* (FM, M, MS); northeast slope of White Top Mt., May 28, 29, 1892, *Small* (FM); mouth of Hungrys Mother Creek, July 4, 1892, *Small* (FM, G, NY, US); Middle Fork of Holston River, Marion, July 6, 1892, *Small* (FM, M, WS).

TENNESSEE. SEVIER CO.: Le Conte, July 4, 1929, *Hudson* (RM).

NORTH CAROLINA. BUNCOMBE CO.: moist soil among rocks, Craggy Mt., May 15, 1898, *ex herb. Biltmore 751a* (G, M, NY, US); thick woods, vicinity of Montreat, Aug. 24, 1913, *Standley & Bollman 9993* (US).

GEORGIA. FLOYD CO.: Rome, *Ravenel* (M).

MICHIGAN. HURON CO.: rich yellow birch woods at base of cliff above Lake Huron, s. e. of Huron City, July 1, 1937, *Anderson & Peck* (WS). MIDLAND CO.: marshy thicket, 2 mi. s. of Midland, May 30, 1927, *Dreisbach 4771* (UM). GRATIOT CO.: Alma, May 16, 1891, *Davis* (MS, UM); Alma, May 26, 1892, *Davis* (UM). ST. CLAIR CO.: open sandy woods near Lake Port, and moist woods near Jeddo, June 30, 1937, *Anderson & Peck* (WS); rich woods near Port Huron, June 5, Aug. 14, 1892, *Dodge* (UM); Port Huron, May, 1888, *ex herb. Glatfelter* (M). OAKLAND CO.: Rochester woods, June 15, 1913, *Farwell 3472* (Farwell); Rochester, May 17, 1914, *Farwell 3624* (Farwell); Parkedale Farm, June 13, 1915, *Farwell 3669* (Farwell, G, M, NY); Walled Lake woods, June 5, 1917, *Farwell 4487, 4489* (Farwell), *4490* (Farwell, G); moist woods, Rochester waterworks, May 15, 1918, *Farwell 4819* (Farwell, G); Marl Lake woods, Sept. 18, 1920, *Farwell 5697* (Farwell); low wet ground, borders of woods, Walled Lake, June 5, 1917, *Farwell & Chandler 4488* (Farwell TYPE of *P. boreale* var. *multiflorum* Farwell); Birmingham, May 25, 1913, *Sutton 292* (UM). WAYNE CO.: woods, Detroit, May 9, 1895, *Farwell 380c* (Farwell), *380d* (Farwell TYPE of *P. boreale* var. *australe* Farwell); Palmer Park woods, Detroit, May 31, 1915, *Farwell 3951* (Farwell), *3952* (Farwell, G, M, NY); Mill Road woods, Redford, May 23, 1920, *Farwell 5447, 5448* (Farwell, G), *5449* (Farwell); Livonia woods, May 21, 1929, *Farwell 8349* (Farwell); Detroit, June, 1870, *Foote* (UM). LIVINGSTON CO.: sandy soil, oak woods, Winants Lake, May 19, 1918, *Ehlers 685* (UM). WASHTENAW CO.: Ann Arbor, May 12, 1860, *ex herb. Almendinger* (UM); third woods, s. e. of Ann Arbor, May 13, 1925, *Emerson* (UM); moist ravine in oak woods, n. of North Lake, May 27, 1925, *Erlanson 1613* (UM); woods near Ypsilanti, May 21, 1891, *Farwell 380b* (Farwell); third woods, near Ann Arbor, May 17, 1926, *Hermann 106* (UM); low elm-oak woods, 5 mi. s. e. of Ann Arbor, July 14, 1935, *Hermann 6892* (FM, MS); Ann Arbor, May 28, *Lewis 73* (UM); Cascade Glen, Ann Arbor, May 24, 1915, *Romein* (UM). INGHAM CO.: woods n. of Agricultural College, May 21, 1894, *Skeels* (MS). JACKSON CO.: without exact locality, May 13, 1897, *ex herb. Camp & Camp* (FM). HILLSDALE CO.: Hillsdale, May 29, 1885, *ex herb. Pelton* (UM). MASON CO.: oak dune, Hamlin Lake, Ludington, Aug. 10, 1910, *Chaney 63* (C, FM, US). MUSKEGON CO.: swamp, Lake Harbor, May 28, 1898, *Umbach* (FM, US). KENT CO.: low rich soil, Grand Rapids, June 1, 1893, *Cole* (Minn); Orchid Swamp, Grand Rapids, May 16, 1897, *Fyfe & Shaddick* (MS). OTTAWA CO.: Holland, Aug., 1910, *Kauffman* (UM). BARRY CO.: Gun Lake, May 30, 1891, *Bailey* (UM). VAN BUREN CO.: ravine, n. of South Haven, Sept. 4, 1911, *Lansing 3334* (FM, G); along river and on wooded hillsides, South Haven, July 18, 1910, *Pennington* (UM). CASS CO.: Hemlock Island, Magician Lake, Aug., 1905, *Pepoon* (MS). BERRIEN CO.: climax forest, Warren Woods,

July 26, 1919, *Billington* (MS, UM), July 30, 1919, *Billington* (UM). CHEBOYGAN CO.: cut-over beech and sugar maple woods, Grapevine Point, Douglas Lake, July 12, 1919, *Deam 28720* (D); same locality, July 19, 1921, *Ehlers 1606* (UM); sandy soil, same locality, June 19, 1922, *Ehlers 1945* (UM); Douglas Lake, July 20, 1911, *Gates 372* (MS); in pineland aspens, Biological Station, July 3, 1917, *Gates & Gates 10476* (M); Grapevine Point, Douglas Lake, July 9, 1929, *Hanna 177* (RM). EMMET CO.: in hardwoods, w. of Pellston, June 22, 1917, *Gates & Gates 10300* (FM, M, RM). CHARLEVOIX CO.: 4½ mi. n. w. of Vanderbilt, July 30, 1912, *Bessey* (MS). ANTRIM CO.: Bellaire, June 6, 1891, *Leavitt* (UM). ALGER CO.: rich deciduous woods above Miners Falls, near Munsing, July 2, 1934, *Fernald & Pease 3240* (G); Chatham, Aug. 22, 1900, *Wheeler* (MS). MARQUETTE CO.: *Acer saccharinum* forest, Turin, May 31, June 5, 1901, *Barlow* (C, G, NY, US), Aug. 21, 1901, *Barlow* (G, MS, US TYPE of *P. cuneatum* Greene); Negaunee, June, 1902, *Rydberg* (NY). KEWEENAW CO.: Cliff Mine woods, June 20, 1886, *Farwell 380, 380a*, Oct. 1, 1914, *Farwell 3909*, July 3, 1915, *Farwell 3995a, 3995b* (Farwell); rich maple woods, 1 mi. w. of Mandan, July 10, 1936, *Hermann 7917* (NY); hard maple woods, Lake Desor trail, Isle Royale, July 10, 1930, *McFarlin 2154* (UM). HOUGHTON CO.: mixed woods, Lake Linden incline, July 5, 1934, *Farwell 9893* (Farwell); Calumet waterworks, June 16, 1926, *Hermann 277* (UM); St. Louis Hill, July 2, 1926, *Hermann 456* (UM). ONTONAGON CO.: woods, south shore of Lake Superior, w. of Ontonagon, Aug., 1937, *Conard* (WS).

WISCONSIN. DOOR CO.: Ephraim, June 5, 1907, *Greenman 2167* (M); Ephraim, May 30, 1926, *Kraus et al.* (G). BROWN CO.: cedar swamp, Green Bay, May 18, 1878, *Schuette* (FM); Upper Peninsula, Green Bay, June 14, 1889, *Schuette* (FM). WASHINGTON CO.: Hartford, June 1, 1929, *Quandt* (WS). MILWAUKEE CO.: Milwaukee, *Hasse* (NY); river bank, Wauwatosa, June, 1890, *Strong* (UM). WALWORTH CO.: Delavan, May, 1866, *Milligan* (US). SAUK CO.: wooded bank, Parfreys Glen, Merrimac, May 23, 1926, *Fassett 3161* (G, NY). ONEIDA CO.: woods, Tomahawk Lake, Minocqua, Aug. 29, 1936, *Peck* (WS). CHIPPEWA CO.: woods, on red clay moraines, n. e. of Chippewa Falls, July 8, 1915, *Butters & Rosendahl 3093* (Minn).

MINNESOTA. COOK CO.: maple forest, Mineral Center, July 5, 1924, *Rosendahl & Butters 4592* (G, Minn, NY). BELTRAMI CO.: Cedar Island, Cass Lake, Aug. 2, 1914, *Pammel & Pammel 575* (G). CLEARWATER CO.: loam, fir and birch woods, Schoolcraft Island, Itasca Park, July 30, 1929, *Grant 2970* (G, Minn, US). HUBBARD CO.: *Populus tremuloides* forest, Benedict, Aug. 28, 1914, *Bergman 3123* (NY, Minn). OTTERTAIL CO.: wet wooded places, Little Pine Lake, Perham, May 30, 1910, *Chandonnet* (D); Lake Lida, Aug., 1892, *Sheldon 3760* (Minn). AITKIN CO.: Nichols, June, 1892, *Sheldon 2107* (Minn). MILLE LACS CO.: Mille Lacs Indian Reservation, June, 1892, *Sheldon 2532* (Minn). HENNEPIN CO.: rich woods, Minneapolis, May, 1892, *Burglehaus* (Minn); prairie, Fort Snelling Reservation, May 30, 1910, *Rosendahl 2462* (Minn). WINONA CO.: Winona, June 9, 1888, *Holzinger* (US TYPE of *P. boreale* Greene); wooded bluffs, without locality, May, 1904, *Holzinger* (Minn).

OHIO. PORTAGE CO.: Newell Ledge, June 16, 1901, *Webb 442* (G), May 10, 1903, *Webb 609* (G). SUMMIT CO.: Peninsula, May 11, 1895, *Moseley* (FM). CUYAHOGA CO.: bank in woods, Berea, June, 1895, *Ashcroft* (RM); Berea, May, 1896, May, 1897, *Ashcroft* (M); Wade Park, Cleveland, May 14, 1912, *Dreisbach 1039* (FM). LORAIN CO.: Oberlin, May 20, 1895, *Ricksecker* (US); rich moist woods, s. of Oberlin, May 21, 1892, *Strong* (UM). ERIE CO.: Cedar Point, May 19, 1893, *Moseley* (UM). OTTAWA CO.: Green Island, Aug. 20, 1940, *Myers* (WVU). RICHLAND CO.: rich damp soils, Mansfield, May 31, 1895, *Wilkinson 10454* (Minn). FRANKLIN CO.: rich wooded hillsides, n. of Columbus, May 13, 1905, *Gleason* (G). CHAMPAIGN CO.: without locality or date, *Samples* (UM). CLARK CO.: Springfield, *Williams* (M). BUTLER CO.: uplands and ravines, Hueston woods, near Oxford, July 9, 10, 1924, *Wehmeyer & Waters 86, 102* (UM).

INDIANA. STEUBEN CO.: low tamarack border of Graveyard Lake, ½ mi. from n. e. corner of state, May 25, 1920, *Deam 30417* (D); black and white oak slope, e. side of Pokagon State Park, May 26, 1927, *Deam 44289A* (D); tamarack bog, ¼ mi. e. of Poka-

gon State Park, May 24, 1929, *Deam 46578* (D). LAGRANGE CO.: Sarah Long woods, along Pigeon River, 2 mi. w. of Mongo, May 17, 1915, *Deam 15702* (D); dry woods, 1½ mi. n. w. of Stroh, June 5, 1915, *Deam 15948, 15957* (D); moist woods, 1½ mi. s. e. of Mongo, May 27, 1920, *Deam 30453* (D). DE KALB CO.: rich damp woods, 1 mi. s. of Garrett, May 17, 1908, *Deam 3034* (D); beech and sugar maple woods, 1 mi. s. of St. Joe, Aug. 17, 1916, *Deam 20849* (D); moist ground in beech and sugar maple woods, ½ mi. s. of St. Joe, May 25, 1920, *Deam 30383* (D); white oak ridge, 2 mi. s. e. of Hamilton, May 25, 1927, *Deam 44279* (D); Truelove woods, 3 mi. e. of Avilla, May 9, 1930, *Deam 48181* (D). NOBLE CO.: woods, 6 mi. s. w. of Rome City, June 20, 1910, *Deam 6780* (D); white oak woods, 4 mi. n. w. of Kendallville, June 6, 1915, *Deam 15848* (D). ALLEN CO.: white oak woods, ½ mi. s. of Viberg Lake, May 31, 1915, *Deam 15826* (Minn); moist woods, 4 mi. e. of Fort Wayne, May 31, 1915, *Deam 15832* (D, Minn). WHITLEY CO.: woods, 2½ mi. s. w. of Coesse, July 5, 1920, *Deam 31181* (D). ADAMS CO.: moist place, woods, 1 mi. w. of Ohio line, 5 mi. s. of Allen Co. line, Aug. 31, 1920, *Deam 32594* (D); rich moist woods of beech, elm and white oak, 3 mi. n. of New Corydon, May 13, 1921, *Deam 33814* (D). WELLS CO.: rich woods, near Bluffton, May 16, 1897, *Deam* (D, FM); rich woods, May 12, 1901, *Deam* (Minn, NY); woods, S. 30, Harrison Tp., May 14, 1905, *Deam* (M, US); Pearce woods, 1½ mi. n. w. of Craigville, Aug. 27, 1924, *Deam 40969* (D). HUNTINGTON CO.: moist woods, 2 mi. n. e. of Buckeye, May 26, 1907, *Deam 1946* (D, Minn); Colvin woods, 1½ mi. e. of Mt. Etna, May 8, 1934, *Deam 54781* (Minn). JAY CO.: beech woods, ¾ mi. n. of Bryant, May 18, 1916, *Deam 19733* (D); Cring woods, 2 mi. n. e. of Portland, July 19, 1923, *Deam 39130* (D); woods, S. 24, 2 mi. n. e. of Pennville, June 8, 1932, *Deam 52044* (D). BLACKFORD CO.: woods, S. 21, 4 mi. n. w. of Hartford City, June 5, 1932, *Deam 51974* (D). RANDOLPH CO.: woods, s. e. of Unionport, May 16, 1916, *Deam 19678* (D); beech woods, 5 mi. n. e. of Lynn, May 16, 1916, *Deam 19693* (D). DELAWARE CO.: woods, 5 mi. w. of Eaton, May 25, 1917, *Deam 23128* (D); same locality, May 27, 1921, *Deam 34086* (D). FAYETTE CO.: beech and sugar maple woods, 1 mi. s. e. of Alpine, May 17, 1921, *Deam 33059* (D); beech woods, 1 mi. n. e. of Orange, May 18, 1921, *Deam 34042* (D). RUSH CO.: woods, 1 mi. w. of Gowdy, May 1, 1922, *Deam 35340* (D); level rich woods, 2 mi. w. of Gowdy, July 7, 1925, *Deam 41395* (D). FRANKLIN CO.: Hillenbrand woods, 2 mi. n. w. of Hamburg, July 20, 1922, *Deam 36935* (D). RIPLEY CO.: woods, 1 mi. s. w. of Versailles, May 3, 1922, *Deam 35372* (D). JENNINGS CO.: beech-liquidambar-red maple woods, 7 mi. s. of Vernon, May 14, 1918, *Deam 24745* (D); red gum-red maple woods on the Frank Hite farm, 4 mi. s. e. of Vernon, Aug. 5, 1932, *Deam 52548* (D). OHIO CO.: wooded slope, along Laughery Creek, S. 5, 1½ mi. s. w. of Farmers Retreat, May 24, 1924, *Deam 40342* (D); wooded slope, along Laughery Creek, 3 mi. w. of Milton, May 9, 1929, *Deam 46567* (D); high wooded bluff, along Laughery Creek, S. 5, 3 mi. s. of Farmers Retreat, May 8, 1931, *Deam 40998* (D). ELKHART CO.: woods, 12 mi. n. w. of Goshen, May 11, 1916, *Deam 19576* (D); woods, 3 mi. s. of Middlebury, May 14, 1919, *Deam 27455* (D, G); black and white oak woods, 3 mi. s. w. of Middlebury, May 27, 1927, *Deam 44321* (D). ST. JOSEPH CO.: beech-white oak woods, 8 mi. w. of South Bend, May 10, 1916, *Deam 19540* (D); woods, 1¼ mi. s. e. of North Liberty, May 5, 1921, *Deam 33711* (D). KOSCIUSKO CO.: Plummer woods, 4½ mi. n. w. of Leesburg, May 14, 1923, *Deam 38271* (D); woods, 7 mi. n. e. of North Manchester, May 18, 1933, *Deam 53607* (D). MARSHALL CO.: woods, s. w. of Lake Maxinkuckee, May 20, 1901, *Clark 1676* (US); n. of Lapaz Junction, May 8, 1913, *Nieuwland 11035* (M). WABASH CO.: white oak, beech and sugar maple woods, 3 mi. n. e. of Disko, May 3, 1921, *Deam 33643* (D). MIAMI CO.: woods, 1 mi. e. of Deedsville, June 8, 1920, *Deam 31081* (D); low beech woods, Larison farm, 2½ mi. s. w. of Amboy, May 26, 1922, *Deam 36199* (D). CASS CO.: rich moist woods, 2½ mi. w. of Lucerne, June 9, 1931, *Deam 50242* (D). GRANT CO.: Leonard woods, 5 mi. n. w. of Upland, May 22, 1915, *Deam 15801* (D); Smith woods, 9 mi. e. of Marion, May 23, 1916, *Deam 19799* (D). HOWARD CO.: rich wooded bank of Wildcat Creek, 2 mi. w. of Greentown, May 15, 1910, *Deam 5947* (D). HAMILTON CO.: wooded hillside, e. of Carmel, May 11, 1913, *Deam 12677* (D). HANCOCK CO.: moist rich woods, 1½ mi. s. e. of Julietta, May 14, 1912, *Deam 10509* (D). MARION CO.: Decatur Tp., April 30,

1905, *Deam* (D). JACKSON CO.: rich beech woods, 1 mi. n. of Chestnut Ridge, April 25, 1910, *Deam 5658* (D); wooded slope, Guthrie Creek, 6 mi. n. of Medora, May 15, 1918, *Deam 24778* (D); wooded ravine, 2 mi. s. e. of Leesville, May 19, 1922, *Deam 35751* (D). WASHINGTON CO.: with beech, base of wooded slope, 6 mi. s. e. of Pekin, S. 24, May 11, 1931, *Deam 50018* (D). LA PORTE CO.: wooded sand dunes, w. of Michigan City, May 22, 1910, *Deam 6427* (D); wooded dunes, e. of Michigan City, May 28, 1913, *Deam 13046* (D); tamarack swamp, ½ mi. n. of Mill Creek, June 4, 1920, *Deam 30750* (D). CARROLL CO.: sugar maple woods, 1½ mi. s. w. of Burnettsville, May 20, 1923, *Deam 38314* (D); beech and sugar maple woods, 1½ mi. w. of Camden, Aug. 17, 1925, *Deam 42136* (D); wooded ravine, 5 mi. n. of Delphi, May 11, 1930, *Deam 48238* (D). TIPPECANOE CO.: in ravines and on hillsides, along river road, La Fayette, May 5, 1900, *Dorner* (D). MONTGOMERY CO.: deep wooded ravines, Sugar Creek, near The Shades, May 16, 1913, *Deam 12779* (D). PUTNAM CO.: woods at alluvial end of lateral ravine, D. P. U. arboretum, Greencastle, May 5, 1935, *Dawson 1136* (Minn); wooded bank, Raccoon Creek, near McGaughey's, June 29, 1913, *Deam 13479* (D); Nelson woods, 10 mi. n. w. of Greencastle, May 23, 1922, *Deam 35974* (D); moist slope in woods, Knoll farm, S. 13, 4 mi. s. e. of Putnamville, May 17, 1926, *Deam 42782* (D). MORGAN CO.: near Monroe Co. line, Monroe-Morgan State Forest, 6 mi. s. of Martinsville, May 22, 1930, *Deam 48364* (D). OWEN CO.: with beech, woods, 3 mi. n. e of Quincy, May 22, 1922, *Deam 35906* (D). MONROE CO.: beech slope, 3 mi. n. w. of Harrodsburg, May 21, 1931, *Deam 50167* (D); Fee pasture, ½ mi. n. e. of Bloomington, 1908, *Pickett* (WS). LAWRENCE CO.: base of hemlock bluff, Back Creek, 2 mi. n. w. of Leesville, May 25, 1930, *Deam 48441* (D). CRAWFORD CO.: wooded base of Evergreen Bluff, 4 mi. s. w. of Grantsburg, June 8, 1919, *Deam 27792* (D, G.) PORTER CO.: Doran woods, 3 mi. s. w. of Lake Michigan, July 10, 1920, *Deam 31487* (D); moist ground, north side of Doran woods, 4 mi. s. w. of Michigan City, May 23, 1923, *Deam 38454* (D). FOUNTAIN CO.: moist woods, 2 mi. n. of Hillsboro, May 24, 1922, *Deam 36037* (D). PARKE CO.: wooded ravine, Sugar Creek, near Turkey Run, Sept. 2, 1911, *Deam 9917* (D). CLAY CO.: wooded bank of creek, 1 mi. e. of Harmony, May 4, 1914, *Deam 12644* (D).

ILLINOIS. COOK CO.: damp woods, Forest Glen, June 4, 1892, *Harper* (WS); woods, near Chicago, June 4, 1892, *ex herb. Moffatt 86* (Minn).

2. Polygonatum cobrense (Wooton & Standley) Gates in Bull. Torr. Bot. Club 44:126, *pl. 6, B.* 1917.

Salomonia cobrensis Wooton & Standley in Contrib. U. S. Nat. Herb. 16:113. 1913.

Perennial herb, 2 to 4 dm. high; rhizome slender; stem slender, somewhat flexuous, glabrous; leaves 10 to 12, alternate, more or less secund, elliptic, 4 to 9.5 cm. long, 0.9 to 3.2 cm. broad, obtuse or slightly acute, narrowed at the base to a broad petiole 3 to 4 mm. long, glabrous, glaucous beneath, very faintly nerved, only the midrib prominent; cauline bract papery, easily detached; peduncles strongly and sharply deflexed, flattened, glabrous, 8 to 15 mm. long, 1- or 2-flowered; pedicels 4 to 16 mm. long, glabrous, sometimes flattened; floral bracts white, papery, narrow, 3 to 6 mm. long, caducous; flowers fragrant, ivory-white, lobes and veins greenish; perianth of mature flower 17 to 23 mm. long, 7 mm. broad, tubular, somewhat expanded toward the mouth, the lobes erect, oblong, obtuse, nearly as long as the tube (about 7 mm. long); filaments slightly papillose, inserted near the middle of the tube; immature fruit pyriform, up to 8 mm. in diameter.

Polygonatum cobrense is easily distinguished from the other North American species. From *P. biflorum* and *P. commutatum* it differs in its papery, caducous

cauline bract and strongly deflexed peduncles. In these characters it resembles *P. pubescens*, from which it differs in its glabrous leaves, large flowers, slightly expanded cylindrical perianth tube, with the filaments inserted near the middle. It is very similar in appearance to the type species of the genus, the European *P. officinale*, and is possibly more closely related to this than to any North American species. Greene must have realized this relationship when he labelled some of his specimens from the Pinos Altos Mountains and Gila Canyon "*Polygonatum vulgare* Desf." [= *P. officinale* All.]—"New to America."

Specimens of *Polygonatum cobrense* were probably the basis for the inclusion of New Mexico and Arizona within the range of *Polygonatum commutatum* as given by Britton & Brown's 'Illustrated Flora' and others.

DISTRIBUTION: Sandy soil on north- and east-facing slopes, or in shade, mountains of Sierra and Grant counties, New Mexico, to southern Navajo County, Arizona.

NEW MEXICO. SIERRA CO.: shady places near Kingston, 1904, *Metcalfe 1036* (US). GRANT CO.: Copper Mines, Santa Rita, June, *Bigelow* (NY, US TYPE); Pinos Altos Mts., May 21, 1880, *Greene 92* (G, M, NYCP); Gila Canyon, April, 1881, *Greene* (FM, G); shady loam, Mimbres River, south end of Black Range, 5500 ft. alt., July 1, 1904, *Metcalfe 1036* (FM, G, M, Minn, NY, US); sandy, usually rocky soil on north- and east-facing slopes or in shade, Canyon of Sapillo Creek, T. 4 or 5 S., R. 14 W., Gila National Forest, June 17, 1938, *Ownbey & Ownbey 1643* (WS, to be distributed); grown at Pullman, Washington, from rhizomes of *Ownbey & Ownbey 1643*, June 10, 1944, *Ownbey* (WS, to be distributed); Copper Mines, 1851, *Wright 1917* (G, NY, US).

ARIZONA. NAVAJO CO.: Ft. Apache, 1893, *Hoyt* (NY).

3. Polygonatum biflorum (Walter) Elliott, Sketch Bot. S. C. & Ga. 1:393. 1817.

Convallaria biflora Walter, Fl. Car., p. 122. 1788.

Polygonatum multiflorum γ. *biflora* Wood, Class-book of Bot., ed. 1, p. 396. 1845.

Salomonia biflora Farwell in Rept. Comm. Parks, Detroit 11:53. 1900.

Polygonatum angustifolium Pursh, Fl. Am. Sept. 1:234. 1814.

Convallaria angustifolia Sprengel, Syst. Veg. 2:96. 1825.

Convallaria canaliculata Mühlenberg in Willdenow, Hort. Berol. 1:45. 1806.

Polygonatum canaliculatum Pursh, Fl. Am. Sept. 1:234. 1814.

Polygonatum multiflorum δ. *canaliculata* Wood, Class-book of Bot., ed. 1, p. 396.1845.

? *Convallaria parviflora* Poiret in Lamarck, Encyc. Méth. Bot. Suppl. 4:29. 1816.

? *Polygonatum parviflorum* A. Dietrich in Otto & Dietrich, Allg. Gartenz. 3:222. 1835.

Polygonatum multiflorum β. *americanum* Hooker, Fl. Bor. Am. 2:176. 1839, probably in part.

Polygonatum biflorum var. *hebetifolium* Gates in Bull. Torr. Bot. Club 44:121. 1917, as to description mostly, and as to specimens cited except the type specimen *ex herb. Chapman* (*pl. 5, A*), and the specimen from Watson, Missouri, which is *P. commutatum*.

Polygonatum hebetifolium Bush in Am. Midl. Nat. 10:391. 1927, excluding name-bringing synonym.

Perennial herb up to about 6 dm. high; rhizome slender; stem slender, erect or arching, upper leafy part usually shorter than lower naked part; leaves alternate, sometimes secund, sessile to semiamplexicaul, elliptic-lanceolate, 4 to 11 cm. long, 0.9 to 3 cm. broad, the upper ones not much shorter than the lower ones, glabrous, paler and glaucous beneath, with 1 to 9 (usually 1 to 5) longitudinal nerves, only

the middle one prominent the entire length of the leaf, the others discernible but often hardly raised and usually fading out in the upper part of the leaf; cauline bract green, leaf-like, persistent; peduncles axillary, solitary, slender, glabrous, arcuate, 1- or 2 (rarely 3)-flowered; pedicels slender, glabrous, subequal, usually shorter than the peduncle; flowers whitish; perianth of mature flower 11 to 19 (usually 13 to 15) mm. long, 3 or 4 mm. broad in pressed material, cylindrical; perianth lobes 3 or 4 mm. long, scarcely spreading; filaments usually minutely papillose, inserted near the middle of the tube.

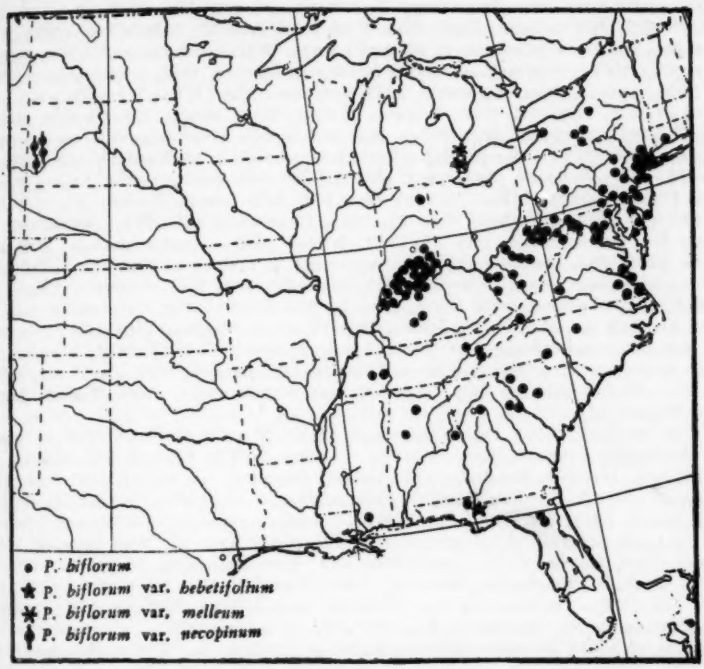
The type specimen of Walter's *Convallaria biflora* is preserved in the British Museum of Natural History. Dr. J. Ramsbottom, Keeper of Botany, has kindly sent a photograph of this specimen, accompanied by the following note by Mr. J. E. Dandy, Assistant Keeper:

> "The specimen is smooth and glabrous throughout (stem, leaves and peduncles). The leaves have dried brown, but the lower surface (as can be seen from the photo.) is paler and slightly glaucescent.
>
> "The specimen agrees with Walter's description except that the leaves are not markedly trinerved. Flowers are absent, but they may have become broken off and lost. It is preserved on fol. 35 of Walter's Herbarium."

It is unfortunate that Gates did not see this specimen, for he misinterpreted Walter's species, considering the very narrow-leaved plants from the Chapman Herbarium (see *P. biflorum* var. *hebetifolium*) as typical. The specimens of the broader-leaved true *biflorum* which he saw, he included in his var. *hebetifolium*. It is because of this misinterpretation that Bush used the name *P. hebetifolium*, raising Gates' variety to specific rank, although the specimens he cited are probably all good *P. biflorum*.

As here interpreted, *Polygonatum biflorum* and its varieties compose the diploid element (n = 10) of the glabrous *P. biflorum*-*P. commutatum* complex of eastern North America. When all of the varieties of *P. biflorum* are considered together, the diploid element of the complex is indeed difficult to distinguish from the tetraploid element, *P. commutatum* (n = 20), except by chromosome number. In general, however, the diploids are smaller in size, daintier in texture, and have fewer and smaller flowers (except var. *hebetifolium*), and fewer prominent leaf nerves (except var. *melleum*); the upper leafy portion of the stem is usually shorter than or equal to the lower naked portion in length (except in var. *necopinum*). All members of the *P. biflorum*-*P. commutatum* complex are separated from the other two species in North America by the green, leaf-like, persistent cauline bract and by the arcuate, not strongly deflexed, peduncles.

The diploids are woodland plants and show little tendency to invade open places, roadsides, fence rows and alluvial soils. Geographically, *Polygonatum biflorum* is less widely distributed than the tetraploid species, and each of its three varieties is highly restricted in range. The present distributions of these four entities suggest that they are all remnants of a once widespread diploid. *P. biflorum* var. *melleum* is found in a small area in Michigan and Ontario, south of Lake Huron, and outside the range of *P. biflorum*. *P. biflorum* var. *hebetifolium* is known from only one locality in western Florida, within a small area which is



Map 2. Distribution of *Polygonatum biflorum* and its varieties. Based on Goode *Base Map* No. 102. By permission of The University of Chicago Press.

already famous for its other endemics, notably *Torreya taxifolia* and *Taxus floridana*. *P. biflorum* var. *necopinum* is restricted to the Black Hills of South Dakota, a region interesting because it is an outpost of the ranges of a number of species of plants, both eastern and western. *P. biflorum* itself, though found over a fairly wide area in eastern United States, also is limited in range. For the most part it is found south of the Wisconsin glacial drift. In Indiana, where the edge of that glaciation is well defined, the species lies wholly south of the boundary, except for a single collection from Allen County. Farther east, the layer of glacial drift is thinner, the boundary is less definite, and some collections from New York, Pennsylvania and Connecticut are apparently within the area of the Wisconsin glaciation.

DISTRIBUTION: Usually in sandy soil, moist to dry woods, Connecticut and New York, south to Florida, west to Indiana, Kentucky, Tennessee and Mississippi (Map 2).

CONNECTICUT. NEW HAVEN CO.: open ledges, top of West Rock, New Haven, June 24, 1932, *Eames 11429* (G).

NEW YORK. ORANGE CO.: Shunemunk Mt., near Mountainville, July 31, 1922, *Denslow* (NY). ROCKLAND CO.: Ramapo, May 24, 1922, *Denslow* (NY). WESTCHESTER

co.: near Bryn Mawr, May 21, 1893, *Bicknell 555* (NY); Larchmont, May, 1891, *Clarke* (NY). NEW YORK CO.: "woods opp. Fire Engine House," New York, June 30, 1894, *Bicknell 557* (NY); Cactus Knoll, New York City, June 22, 1899, *Clute* (NY). SUFFOLK CO.: hilly rich woods, n. of Motor Parkway, Wyandanch, June 2, 1925, *Ferguson 3762, 3763* (NY); hilly dry oak woods, Northport, May 21, 1927, *Ferguson 5447* (NY); dry hilly woods, Smithtown, June 9, 1927, *Ferguson 5572* (NY); dry hilly woods, Cold Spring Harbor, Aug. 31, 1926, *Ferguson 6013* (NY). NASSAU CO.: woods, Merrick, May 27, 1921, *Ferguson 127* (NY); rich wet woods, Meadowbrook, June 10, 1925, *Ferguson 3786* (NY); edge of plains, East Meadowbrook, s. of Westbury and Hicksville, June 20, 1927, *Ferguson 5652, 5653* (NY); hilly rich woods, Locust Valley, June 7, 1928, *Ferguson 6590* (NY). QUEENS CO.: high hilly woods, Queens, May 30, 1913, *Bicknell 558* (NY); Flushing, May 29, 1925, *Ferguson 3744* (NY). RICHMOND CO.: Princes Bay, Staten Island, May 25, 1889, *Britton* (NY). ONONDAGA CO.: Onondaga Valley, June, 1890, *Underwood* (NY). TOMPKINS CO.: shore of Beebe Lake, Fall Creek Ravine and vicinity, Ithaca, May 27, 1915, *Alexander 3745* (G); cemetery, Ithaca, June 8, 1892, *Durand* (Minn); Fall Creek, June 9, 1893, *Schrenk* (M); dry ravine bank, between Renwick and McKinney's, Ithaca, June 18, 1916, *Wiegand 6198* (G). SCHUYLER CO.: dry oak-cornel hillside, e. of Montour Falls, Montour, Sept. 23, 1917, *Wiegand 7886* (M). CHEMUNG CO.: rich woods, without locality, June 3, 1896, *Lucy 2642* (FM). ERIE CO.: Buffalo, *Clinton* (G). COUNTY NOT DETERMINED: South Harbor, June 9, 1895, *Howell* (M).

NEW JERSEY. BERGEN CO.: moist woods, Carlstadt, 1877, *Oehler* (NYCP). PASSAIC CO.: Boardville, Pompton, May 31, 1923, *Denslow* (NY); railroad embankment, near Hewitt, Sept. 17, 1923, *Denslow* (NY); Haskell, Pompton, June 6, 1927, *Denslow* (NY). MORRIS CO.: woods, Chatham, May 30, 1903, *Mackenzie 189* (NY); dry woodlands, Budd Lake, June 9, 1918, *Mackenzie 8321* (NY). HUDSON CO.: Snake Hill, near Hoboken, June 2, 1884, *Schrenk* (M). UNION CO.: Plainfield, June 12, 1892, *Morong* (NY); Summit, June, *Slosson* (WS). MIDDLESEX CO.: New Brunswick, May, 1894, *Blodgett* (NY); sandhills, Woodbridge, May 30, 1890, *Churchill* (G); New Brunswick, June, 1888, *Vail* (NY). MONMOUTH CO.: Freehold, June 2, 1854, *Walters* (UM). MERCER CO.: Pennington Mt., Hopewell, June 17, 1924, *Denslow* (NY). CAMDEN CO.: rich thicket, e. of North Branch of Newton Creek at A. C. R. R., West Collingswood, May 22, 1926, *Adams 190* (M); thickets, Gloucester, May 30, 1922, *Dreisbach 2-83* (FM); roadside, Albion, June 7, 1926, *Meredith* (NY). GLOUCESTER CO.: sandy fields and fence rows near the lighthouse, Washington Park, May 24, 1910, *Long 3509* (G). CAPE MAY CO.: moist sandy woods, Cape May Point, June 3, 1928, *Benner* (G).

PENNSYLVANIA. MONROE CO.: Naomi Pines, Pocono Plateau, June 7-10, 1889, *Britton* (NY). LEHIGH CO.: woods, 1⅛ mi. w. by s. w. of Wescosville, May 8, 1921, *Pretz 10665* (NY). BUCKS CO.: woods, 2 mi. n. w. of Doylestown, May 31, 1925, *Dreisbach 3497* (UM); West Rockhill Tp., near Telford, June 13, 1926, *Strohm* (G). MONTGOMERY CO.: Bryn Mawr, May, 1887, *Southworth* (UM). PHILADELPHIA CO.: woods, East Fairmount Park, Philadelphia, May 17, 1877, *Redfield 8186* (M). CHESTER CO.: West Chester, 1827, *Darlington* (NY); woods, Westtown Farm, May 24, 1905, *Wildman 172* (US). LANCASTER CO.: Mountville, July, 1888, *Eby* (M); limestone, on the Little Conestoga Creek beyond Millersville, May 31, 1901, *Heller* (FM, G, US); limestone, woods below Graeffs Landing, Sept. 14, 1901, *Heller* (US); woods and thickets, Mountalto, June 6, 1906, 1908, *Illick* (M). DAUPHIN CO.: woods, near Steelton, July 18, 1888, *Small* (FM). YORK CO.: Conewago Creek, May, 1898, *Eisenhower* (M); without locality, June 3, 1895, *Glatfelter* (M); without locality, June 3, 1895, *Williams* (M). BLAIR CO.: Rattlesnake Mt., Tyrone, Aug. 20, 1915, *Anderson* (G). WESTMORELAND CO.: Shades Ravine, North Trafford, May 29, 1937, *Emig* (M). FAYETTE CO.: woodlands, Ohiopyle, May 23, 1936, *Bright 13652* (WS).

DELAWARE. NEW CASTLE CO.: woods, Townsend, May, 1890, *Canby* (Minn); Brandywine River, Wilmington, May 10, 1886, *Leeds* (FM). SUSSEX CO.: dry sandy soil, without locality, Sept. 8, 1887, *Canby* (NY).

MARYLAND. WICOMICO CO.: sandy woods, Salisbury, Aug., 1889, *ex herb. Canby* (NYCP). BALTIMORE CO.: without locality, May 23, 1878, *Smith* (US). ALLEGANY

CO.: Cumberland, 1894, *Shriver* (NY). MONTGOMERY CO.: rich rocky woods, near Widewater, below Greatfalls, May 10, 1916, *Kearney & Maxon 77* (US); Cabin John Run, May 18, 1897, *Pieters* (UM); Glen Echo, May 19, 1895, *Pollard 261* (US); damp woods, opposite Plummers Island, May 9, 1915, *Standley 11410* (US); Plummers Island, in the Potomac River, near Cabin John, May 9, 1915, *Standley 11473* (US). PRINCE GEORGES CO.: Laurel, June 3, 1897, *Knowlton* (US); low woods at edge of swamp, e. of Sunnyside, June 7, 1918, *Maxon 6420* (US).

DISTRICT OF COLUMBIA. Woods, Chevy Chase road, near Reno, May 25, 1904, *Chase 2222* (FM, MS); in woods n. of Military Road, Rock Creek Park, May 25, 1915, *Maxon & Standley 143* (US); Rock Creek Park, May 14, 1896, *Steele* (US); low ground, May 10, 1897, *Steele* (Minn); Piney Branch, May 9, 1895, *Topping* (Minn); Rock Creek, May 15, 1872, June 16, 1878, *Ward* (US); vicinity of Washington, Aug. 20, 1876, *Ward* (US).

VIRGINIA. ARLINGTON CO.: Clarendon, May 25, 1928, *Blake 10576* (WS); Fort Myer, May 14, 1896, *Mearns* (US). GLOUCESTER CO.: vicinity of Capahosic, May 26, 1914, *Van Eseltine 141* (US). JAMES CITY CO.: rich soil of beech slope, ½ mi. w. of Williamsburg, May 11, 1920, *Grimes 2577* (NY); deep wooded ravine, 2 mi. s. e. of Williamsburg, Apr. 21, 1921, *Grimes 3472* (NY); rich wooded hillside, 1 mi. s. e. of Williamsburg, May 2, 1921, *Grimes 3529* (G, NY). ELIZABETH CITY CO.: damp thicket, Hampton, May 7, 1903, *Miller* (US). PRINCESS ANNE CO.: rich woods, Great Neck, May 5, 1935, *Fernald & Griscom 4356* (G); rich deciduous woods, e. of Little Creek, July 31, 1934, *Fernald & Long 3857* (G); dry mixed woods, Little Neck, Aug. 8, 9, 1934, *Fernald & Long 3858* (G); recently cleared sandy knoll, Virginia Beach, May 9, 1903, *Miller* (US). NORFOLK CO.: near Norfolk, May 21, 1898, *Kearney 1310* (US). SOUTHHAMPTON CO.: sandy alluvial bottomlands of Three Creek, Drewryville, June 22, 23, 1936, *Fernald, Long & Smart 5718* (G). SUSSEX CO.: sandy and loamy woods, s. of Pleasant Grove Church, July 22, 1936, *Fernald & Long 6157, 6158* (G). BEDFORD CO.: dry woods, without locality, May 10, 1871, *Curtiss* (G). SMYTH CO.: vicinity of Marion, May 19, 1892, *Britton, Britton & Vail* (NY); slopes and summit of Pond Mt., East Marion, June 11, 1892, *Small* (FM).

WEST VIRGINIA. BERKELEY CO.: Camp Frame, May 16, 1937, *Shreve* (WVU). MORGAN CO.: summit of Cacapon Mt., July 9, 1937, *Core 5783* (WVU). HAMPSHIRE CO.: Hanging Rock, May 26, 31, June 15, 28, 1932, *Frye 605, 540, 492, 1062a* (WVU). MINERAL CO.: Ridgeville, May 31, 1940, *Southern Appalachian Botanical Club Foray* (WVU). PRESTON CO.: Lake Terra Alta, June 6, 1937, *Tighe, Conrad & Bergner* (WVU). MONONGALIA CO.: Morgantown, May 31, 1926, *Humphrey 788* (WVU). TAYLOR CO.: Wendel, May 29, 1940, *Davis & Davis 3970* (WVU). HARRISON CO.: Shinnston, July 29, 1933, *Martin 216* (WVU). WETZEL CO.: woods, between Hundred and Littleton, June 9, 1931, *Haught 349* (WVU). BRAXTON CO.: Little Birch, June 1, 1933, *Harris* (WVU). CALHOUN CO.: Sycamore, June 1, 1933, *Harris* (WVU). WIRT CO.: 1 mi. above mouth of Reedy Creek, June 23, 1934, *Bartholomew 94* (WVU). WOOD CO.: Parkersburg, July 19, 1929, *W. V. U. Botanical Expedition* (G). KANAWHA CO.: Gilligans Hill, May 30, Watts Hill, Aug. 9, 1934, *Greenlee* (WVU). LINCOLN CO.: forest above Miller School, July 1, 1930, *Berkley 907* (M). WAYNE CO.: 1 mi. n. of Ft. Gay, Nov. 22, 1931, *Lycan 13* (WVU). MINGO CO.: Kermit, June 3, 1933, *Harris* (WVU). RALEIGH CO.: along hollow, up Madams Creek, May 27, 1940, *Tosh 118* (WVU).

NORTH CAROLINA. ORANGE CO.: vicinity of Chapel Hill, May, 1898, *Ashe* (NY). MECKLENBURG CO.: dry woods, Charlotte, Apr. 26, 1924, *Knowlton* (G).

SOUTH CAROLINA. ANDERSON CO.: Watson woods, near Anderson, May 10, 1920, *Davis 5102, 7021* (M), *7698* (UM); Norris farm, near Anderson, Aug. 7, 1919, *Davis 9871* (M); dry oak woods, 6 mi. n. of Anderson, Aug. 20, 1927, *Wiegand & Manning 804* (G). GREENWOOD CO.: Greenwood, Aug. 24, *Davis* (M). LEXINGTON CO.: vicinity of Batesburg, Apr. 29, 1911, *McGregor 22* (US).

GEORGIA. RICHMOND CO.: clay soil, ravine, Augusta, Apr. 25, 1903, *Cuthbert* (UF); ravine, Raes Creek, Augusta, Apr. 29, June 6, 1904, *Cuthbert* (UF). MCDUFFIE CO.: wooded hillside near branch, vicinity of Thomson, Sept. 8, 1907, *Bartlett 986* (UM),

Aug. 9, 1909, *Bartlett 1713* (D). DE KALB CO.: Stone Mt., May 1-18, 1895, *Small* (NY).

FLORIDA. ALACHUA CO.: Buzzards Roost, Gainesville, May 3, 1936, *Arnold & West* (UF); same locality, May 2, 1928, *West* (UF). MARION CO.: McIntosh, Apr. 8, 1926, *Miller 532* (US). JACKSON CO.: hammock along Blue Springs, n. of Marianna, Mar. 17, 1937, *Exploration Party 1937* (UF); Chipola River, Marianna, July 20, 1936, *Hume* (UF).

ALABAMA. CULLMAN CO.: Cullman, Aug. 25, 1891, *Mohr* (US). TUSCALOOSA CO.: Tuscaloosa, Apr. 4, 1874, *ex herb. Mohr* (US); Tuscaloosa, Apr. 10, 1874, *Smith* (US). LEE CO.: Auburn, Apr. 17, 1897, *Earle & Baker* (NY); Auburn, Apr. 22, 1896, *Earle & Underwood* (NY).

MISSISSIPPI. HANCOCK CO.: Crane Creek, Apr. 3, 1918, *Johnson* (Farwell).

INDIANA. ALLEN CO.: wooded ravine, Robinson Park, 6 mi. n. e. of Ft. Wayne, June 3, 1906, *Deam 1054* (D). FAYETTE CO.: beech-sugar maple woods, 1 mi. s. e. of Alpine, May 16, 1921, *Deam 33939* (D). FRANKLIN CO.: Bane woods, 1½ mi. s. w. of Metamora, May 17, 1921, *Deam 33995* (D); Hillebrand woods, 2 mi. s. w. of Metamora, July 21, 1922, *Deam 36954* (D). DEARBORN CO.: beech-white oak woods, 3½ mi. s. e. of Sunman, May 19, 1919, *Deam 27561* (D); white oak-beech woods, 1 mi. s. w. of Farmers Retreat, May 24, 1924, *Deam 40352* (D). JENNINGS CO.: white oak woods, 2 mi. e. of Grayford, May 30, 1923, *Deam 38594* (D); woods, 3 mi. s. w. of Scipio, May 9, 1924, *Deam 40087* (D). JEFFERSON CO.: low flat woods, 2½ mi. n. e. of Kent, May 30, 1930, *Deam 48573* (D). SCOTT CO.: beech-sugar maple woods, 1 mi. n. of Lexington, May 20, 1919, *Deam 27585* (D, Farwell, G); beech woods, 1½ mi. n. of Lexington, May 5, 1922, *Deam 35422, 35439* (D); beech woods, along Kinberlin Creek, 4 mi. w. of Lexington, May 12, 1924, *Deam 40117* (D); beech slope, low woods of Chas. Shields, 1½ mi. w. of Lexington, May 15, 1927, *Deam 44241* (D). CLARK CO.: deep wooded ravine, just n. of tract 15, Clark Co. State Forest, May 11, 1910, *Deam 5864* (D); white oak woods, without locality, May 25, 1919, *Deam 27603* (Farwell). BARTHOLOMEW CO.: beech woods, 6 mi. n. w. of Columbus, June 5, 1921, *Deam 264* (D). BROWN CO.: woods, between Helmsburg and Nashville, May 21, 1910, *Deam 5983* (D); beech slope, 1 mi. w. of Georgetown [Bean Blossom], May 22, 1930, *Deam 48381* (D); white oak slope, 2 mi. e. of Helmsburg, May 22, 1930, *Deam 48386* (D). JACKSON CO.: wooded slope, south side of Guthrie Creek, 6 mi. n. of Medora, May 15, 1918, *Deam 24773* (D). WASHINGTON CO.: woods, Wright farm, 5 mi. s. e. of Salem, May 20, 1924, *Deam 40240* (D). HARRISON CO.: woods, 5 mi. s. e. of Milltown, June 25, 1915, *Deam 16434* (D); woods, 2 mi. n. e. of Corydon, June 3, 1917, *Deam 23384* (D); rich woods, 2½ mi. s. e. of Palmyra, June 4, 1917, *Deam 23424* (D); wooded slopes, Elizabeth, June 11, 1919, *Deam 27887* (Farwell); wooded slope of Elizabeth Hill, 3 mi. e. of Elizabeth, May 10, 1922, *Deam 35516* (D). MONROE CO.: beech woods, ¾ mi. n. w. of Harrodsburg, June 9, 1917, *Deam 23573* (D); woods, ½ mi. w. of Stanford, Aug. 8, 1918, *Deam 26072A* (D); wooded ravine, 11 mi. n. e. of Bloomington, May 21, 1922, *Deam 35851* (D); wooded sandstone slope, 3 mi. s. of Stanford, May 21, 1931, *Deam 50173* (D). GREENE CO.: sandy soil, sugar maple woods, 1 mi. n. of Newberry, July 3, 1918, *Deam 25659* (D). LAWRENCE CO.: woods, Donaldson farm, 3 mi. s. e. of Mitchell, July 12, 1915, June 8, 1917, *Deam 17282, 23525* (D); woods along Guthrie Creek, 1¼ mi. n. e. of Tunnelton, May 17, 1918, *Deam 24844* (D). MARTIN CO.: wooded cliff of White River, 2 mi. above Shoals, May 20, 1913, *Deam 12875* (D); wooded hillside, 2 mi. n. e. of Loogootee, July 10, 1915, *Deam 17140* (D). DAVIESS CO.: beech-white oak woods, 1 mi. n. e. of Portersville, June 11, 1929, *Deam 46831* (D); black and white oak ridge, 2 mi. n. e. of Corning, May 18, 1931, *Deam 50120* (D). ORANGE CO.: with beech, wooded slope, Meissen woods, 6 mi. s. e. of Paoli, May 14, 1922, *Deam 35652, 35668* (D). DUBOIS CO.: dry woods, 3½ mi. s. w. of Huntingburg, May 4, 1919, *Deam 27234* (D, Farwell); moist white oak woods, 3 mi. s. w. of Huntingburg, May 4, 1919, *Deam 27239* (D); crest of black and white oak woods, 2 mi. e. of Holland, May 29, 1926, *Deam 43050* (D). PERRY CO.: black and white oak woods, 7 mi. n. e. of Tell City, May 3, 1927, *Deam 44179* (D); with beech, base of a black and white oak slope, 6 mi. up Deer Creek from its mouth, May 6, 1929, *Deam 46546* (D); dry wooded slope, 5 mi. n. w. of Rome, Aug. 10, 1931, *Deam 50908* (D). WARRICK CO.: woods, 1½ mi. e. of New-

burg, June 11, 1918, *Deam 25335* (D). GIBSON CO.: Mauck woods, 4 mi. s. e. of Princeton, June 30, 1918, *Deam 25532* (D). POSEY CO.: very sandy woods, Dransfield farm, 3 mi. s. of New Harmony, Sept. 27, 1926, *Deam 43841* (D).

KENTUCKY. JEFFERSON CO.: Louisville, 1835, *Short* (M). MEADE CO.: damp hillside by brook, Grahampton, near Fort Knox, Apr. 30, 1933, *Carleton 245* (G). EDMONSON CO.: moist ravine, Chalybeate, May 8, 1936, *Shacklette 309* (G). WARREN CO.: Bowling Green, May 29, 1899, *Price* (M).

TENNESSEE. KNOX CO.: rich wooded bluffs, Knoxville, June, 1897, *Ruth 1172* (NY). BLOUNT CO.: Sunshine, June 5, 1929, *Hudson 173* (RM). ROANE CO.: Oliver Springs, May 3, 1890, *Lamson-Scribner* (US). DECATUR CO.: without locality, May, 1855, *ex herb. Ames* (UM). MADISON CO.: rich woods, Jackson, May, 1892, *Bain 307* (NY).

STATE NOT DETERMINED. Photograph of TYPE in the British Museum Herbarium (M).

3a. Polygonatum biflorum var. **melleum** (Farwell) R. Ownbey, n. comb.

Polygonatum melleum Farwell in Rept. Mich. Acad. Sci. 20:170. 1918.

Perennial herb, usually less than 6 dm. high; rhizome slender; stem slender, arching, upper leafy part usually about equalling lower naked part in length; leaves alternate, elliptic-lanceolate to short-elliptic, sessile to distinctly short-petiolate, 2.5 to 16 cm. long, 1 to 8.5 cm. broad, glabrous, dark green above, glaucous and paler beneath, with 5 to 11 nerves all of nearly equal prominence and all fading out above the middle of the leaf; cauline bract green, leaf-like, persistent; peduncles axillary, solitary, flattened, glabrous, arcuate, 2- to 4-flowered; pedicels unequal, equal to or shorter than the peduncle; flowers honey-yellow, 12 to 15 mm. long; filaments somewhat papillose to densely so, inserted near the middle of the perianth tube; immature berries up to 8 mm. in diameter.

Polygonatum biflorum var. *melleum* differs from *P. biflorum* in having many-nerved leaves, more and smaller flowers, and very nearly equal upper leafy and lower naked portions of the stem. The type specimen and plants like it may easily be distinguished also by the strikingly short and elliptic leaves, 2.1 to 2.5 times as long as broad, as opposed to 2.9 to 3.6 times in *P. biflorum*, and by a great difference in length between the lower and upper leaves of the same plant; in *P. biflorum* the lower leaves are usually 1.1 to 1.5 times as long as the upper ones; in typical var. *melleum* they are 2.1 to 2.4 times as long. A mass collection from the type locality of *P. biflorum* var. *melleum*, statistically studied, reveals, however, that this variety is extremely variable. Some individuals are indistinguishable from *P. biflorum*, while others are difficult or impossible to separate, on morphological criteria, from *P. commutatum*. Thus it cannot be considered to be a species.

DISTRIBUTION: Restricted to the region about Lake St. Clair, south of Lake Huron, in Michigan and Ontario (Map 2). At the type locality, at least, it is found on the beach of an ancient glacial lake.

MICHIGAN. ST. CLAIR CO.: open woods, glacial lake beach, near Algonac, June 30, 1937, *Anderson & Peck* (mass collection); open woods, Algonac, June 16, 1915, *Farwell 3974* (Farwell TYPE); Algonac, Sept. 15, 1900, *Dodge* (UM).

ONTARIO. ESSEX CO.: Sandwich, July 25, 1901, *Macoun 54099* (MS).

3b. Polygonatum biflorum var. **hebetifolium** Gates in Bull. Torr. Bot. Club 44:121, *pl. 5, A.* 1917, as to specimen cited as the type.

Polygonatum hebetifolium Bush in Am. Midl. Nat. 10:391. 1927, as to name-bringing synonym only.

Polygonatum biflorum sensu Gates in Bull. Torr. Bot. Club 44:120, *pl. 4, B.* 1917.

Perennial herb; stem simple, 4 to 5 dm. high, glabrous; leaves alternate, subsecund, semiamplexicaul, oblong-lanceolate, 5 to 9 times as long as broad, 6.5 to 13 cm. long, 0.8 to 2 cm. broad, the upper ones nearly as long as the lower ones, glabrous, with from 3 to 7 nerves of which only the middle one extends the full length of the leaf; cauline bract green, leaf-like, persistent; peduncles axillary, solitary, 12 to 35 mm. long, slender, glabrous, arcuate, 1- or 2-flowered; pedicels subequal, 3 to 15 mm. long, shorter than the peduncles, glabrous; flowers large, 20 to 23 mm. long, yellowish when dry; filaments minutely papillose, the free part shorter than the anthers.

Polygonatum biflorum var. *hebetifolium* is quite distinct from *P. biflorum* because of the long narrow leaves, 5 to 9 times as long as broad, the long slender flexuous peduncles, and the large flowers. It belongs, without question, to the *P. biflorum-P. commutatum* complex. Its morphological characteristics suggest that it is diploid, and as such it must be considered to be a variety of *P. biflorum*. The stomates, however, are even larger than is usual in the tetraploid *P. commutatum*. If it should be found to be tetraploid also, it must stand as a third species of this complex, taking the name *P. hebetifolium*. Attempts to secure living material for cytological study were unsuccessful. Mr. Leslie Hubricht looked for plants in its only known locality, and reported the native vegetation largely destroyed by wild pigs.

The only specimens of this variety known to the writer are several sheets from Chapman's herbarium in the Herbarium of the Missouri Botanical Garden. The one chosen by Gates as the type specimen has immature flowers and lacks data as to name of collector and place and time of collection. The other specimens include two sheets of plants collected in rich shady woods at Aspalaga, Florida, April, 1898, and a set of six sheets of very uniform specimens lacking collection data. These six are cited by Gates as typical of his conception of Walter's *Convallaria biflora*. Another sheet contains one specimen like those on the six sheets mentioned and one specimen with slightly broader leaves. This last plant Gates mentions in his discussion of the variety. All the other specimens cited by Gates with the original description are *P. biflorum*, except the plant from Watson, Missouri *(Bush 527)*, which is *P. commutatum*. It is unfortunate that Gates selected one of the Chapman specimens to typify his variety *hebetifolium* when he referred the rest of them to *P. biflorum*. It is quite obvious that his intention was to separate the broad-leaved plants (true *C. biflora* Walter) as the variety, and it is to this broad-leaved element that the descriptive name *"hebetifolium"* (blunt-leaved) refers. Only the specimen which was designated as the type ties the inappropriate varietal name *hebetifolium* to the narrow-leaved entity.

Gates, for no apparent reason, except that Walter originally described *Convallaria biflora* in his 'Flora Caroliniana', states that the Chapman plants "doubtless came from somewhere in the southeastern states, probably North Carolina."

It seems much more likely that they were collected in western Florida, where Chapman lived, especially since two sheets in the group are so labelled.

DISTRIBUTION. Rich shady woods. Known from only one locality, along the Apalachicola River at Aspalaga, western Florida (Map 2).

FLORIDA. LIBERTY CO.: rich shady woods, Aspalaga, Apr., 1898, *ex herb. Chapman* (M). COUNTY NOT DETERMINED: without locality or date, *ex herb. Chapman* (M 138701 TYPE); without locality or date, *ex herb. Chapman* (M).

3c. Polygonatum biflorum var. necopinum R. Ownbey, n. var.[42]

Perennial herb about 6 dm. high; rhizome slender; stem slender, nearly erect, upper leafy part longer than lower naked part; leaves alternate, short-petiolate, elliptic-lanceolate, 6.5 to 10 cm. long, 1.8 to 4 cm. broad, glabrous, paler and glaucous beneath, with 1 to 7 longitudinal nerves, only the midrib prominent the full length of the leaf; cauline bract green, leaf-like, persistent; peduncles axillary, solitary, slender, flattened, glabrous, arcuate, 2-flowered; pedicels slender, glabrous, subequal, shorter than the peduncle; flowers whitish, 15 to 17 mm. long, 5 or 6 mm. broad in pressed material, cylindrical, perianth lobes 4 mm. long, scarcely spreading; filaments nearly smooth, inserted near the middle of the tube.

Polygonatum biflorum var. *necopinum* is taller and has flowers a little larger than is usual in *P. biflorum*, and the upper leafy portion of the stem is considerably longer than the lower naked portion. Its habitat is on limestone rather than in sandy soil. Geographically it is found far outside the range of *P. biflorum*. Except for its diploid chromosome number it is very much like many plants of the tetraploid *P. commutatum*.

DISTRIBUTION. On limestone, deciduous woods along streams, foothills canyons of the Black Hills of western South Dakota (Map 2).

SOUTH DAKOTA. MEADE CO.: Black Hills, near Ft. Meade, July 27, 28, 1887, *Forwood 348* (C, US). LAWRENCE CO.: Lead City, July 16, 1892, *Rydberg 1039* (US). PENNINGTON CO.: Rapid Creek and Dark canyons, Rapid City, June 13, 1927, *Hayward 821* (FM, RM); grown from rhizomes collected in Rapid Creek Canyon, 1 to 3 miles above Canyon Lake, moist shady slope under oaks and elms, limestone formation, June, 1939, *Ownbey & Ownbey* (M TYPE, WS). CUSTER CO.: in shade, along stream, State Game Lodge, June 26, 1924, *McIntosh 408* (RM).

4. Polygonatum commutatum (Schultes f.) A. Dietrich in Otto & Dietrich, Allg. Gartenz. 3:223. 1835.

Convallaria commutata J. H. Schultes in Schultes & Schultes, Syst. Veg. 7[2]:1671. 1830.
Polygonatum latifolium var. *commutatum* Baker in Journ. Linn. Soc. [Lond.] Bot. 14:555. 1875.
Polygonatum biflorum var. *commutatum* Morong in Bull. Torr. Bot. Club 20:480. 1893; Mem. Torr. Bot. Club 5:115. 1894.

[42] **Polygonatum biflorum** var. **necopinum**, var. nov. Herba perennis ad 6 dm. alta; radice subtenui; cauli subtenui prope erecto, parte superiori foliosa quam parte inferiori nuda longiori; foliis alternis brevi-petiolatis elliptico-lanceolatis, 6.5–10 cm. longis, 1.8–4 cm. latis, glabris, subtus pallidioribus glaucisque, 1–7-nerviis, medio-nervo solo prominente per totam longitudinem foliorum; bractea caulina viridi foliacea persistente; pedunculis axillaribus solitariis tenuibus compressis glabris arcuatis bifloris; pedicellis tenuibus glabris subaequalibus quam pedunculo brevioribus; floribus subalbidis, 15–17 mm. longis, 5 vel 6 mm. latis, cylindricis, laciniis 4 mm. longis leviter patentibus; filamentis subglabris, prope tubi medium insertis.

Salomonia commutata Farwell in Rept. Comm. Parks, Detroit 11:53. 1900.
Polygonatum latifolium Pursh, Fl. Am. Sept. 1:235. 1814, not *P. latifolium* (Jacq.) Desf. in Ann. Mus. Par. 9:50. 1807.
Polygonatum multiflorum ε. *latifolia* Wood, Class-book of Bot., ed. 2, p. 553. 1847.
Polygonatum giganteum A. Dietrich in Otto & Dietrich, Allg. Gartenz. 3:222. 1835.
Convallaria gigantea Hort. ex Dietrich, *l. c.*, as synonym.
Polygonatum multiflorum γ. *giganteum* Wood, Class-book of Bot. Fl. U. S. & Can., p. 714. 1861.
Polygonatum canaliculatum β. *giganteum* Miquel in Ann. Mus. Bot. Lugduno-Batavi 3:148. 1867.
Polygonatum biflorum β. *giganteum* Wood, Am. Bot. and Flor., p. 346. 1870.
Polygonatum canaliculatum var. *giganteum* Farwell in Bull. Torr. Bot. Club 42:256, *pl. 18*. 1915; Am. Midl. Nat. 11:78. 1928.
Polygonatum multiflorum β. *americanum* Hooker, Fl. Bor. Am. 2:176. 1839, probably in part.
Polygonatum canaliculatum var. *americanum* Farwell in Bull. Torr. Bot. Club 42:256, *pl. 17, B.* 1915; Am. Midl. Nat. 11:77. 1928.
Polygonatum virginicum Greene, Leaflets 1:181. 1906.
Polygonatum biflorum virginicum Farwell in Bull. Torr. Bot. Club 42:254, *pl. 15, B.* 1915.
Polygonatum commutatum virginicum Gates in Bull. Torr. Bot. Club 44:123, *pl. 6, A.* 1917.
Polygonatum biflorum var. *ovatum* Farwell in Bull. Torr. Bot. Club 42:255, *pl. 16, A.* 1915.
Polygonatum commutatum ovatum Gates in Bull. Torr. Bot. Club 44:124. 1917.
Polygonatum ovatum Bush in Am. Midl. Nat. 10:397. 1927.
Polygonatum canaliculatum var. *ovatum* Palmer & Steyermark in Ann. Mo. Bot. Gard. 22:503. 1935.
Polygonatum ellipticum Farwell in Bull. Torr. Bot. Club 42:255, *pl. 16, B.* 1915.
Polygonatum commutatum var. *lineamentosum* Lunell in Am. Midl. Nat. 5:94. 1917.
Polygonatum canaliculatum var. *americanum* subvar. *ellipticum* Farwell in Am. Midl. Nat. 11:78. 1928.
Polygonatum canaliculatum var. *oblongifolium* Farwell in Rept. Mich. Acad. Sci. 22:181. 1921.
Polygonatum commutatum f. *ramosum* McGivney in Am. Midl. Nat. 9:664. 1925.
Polygonatum canaliculatum f. *ramosum* Clute in Am. Bot. 49:73. 1943.
Polygonatum biflorum f. *ramosum* Fernald in Rhodora 46:12. 1944.
Polygonatum biflorum var. *ovatum* subvar. *ellipsoidale* Farwell in Am. Midl. Nat. 11:78. 1928.

Perennial herb, 0.5 to 2 m. high, rarely smaller; rhizome stout, often branched; stem usually stout, arching, upper leafy part longer than lower naked part; leaves 11 to 25, alternate, amplexicaul, varied in shape, ovate-lanceolate, elliptic-lanceolate, oblong-lanceolate, or broadly oval, 6 to 18 cm. long, 1.5 to 10 cm. broad, glabrous, dark green above, glaucous and paler beneath, with 7 to 19, or more, major nerves, prominent the full length of the leaf, often so strong that the leaf is grooved on the upper surface, the major nerves alternating with other fainter, but distinct, nerves; cauline bract green, leaf-like, persistent; peduncles coarse, flattened, often stiff and wiry, usually long and arched, glabrous, 1- to 15-flowered; pedicels subequal to sometimes very unequal, usually shorter, but sometimes longer, than the peduncle; flowers yellowish green to greenish white, tipped with green, 14 to 23 mm. long, 3 to 7 mm. broad, perianth lobes more or less spreading; filaments smooth to densely papillose, inserted near the middle of the perianth tube; berries dark blue, 8 to 12 mm. in diameter.

Polygonatum commutatum represents the tetraploid element of the *P. biflorum-P. commutatum* complex. Although known under the name *P. commutatum* for nearly a century, this species has in recent years been passing under the name *P. canaliculatum*. During the early part of this work the latter name was mistakenly applied to this tetraploid element by the present writer. Since nearly all of the herbarium study was done at this time, specimens of *P. commutatum* in many herbaria were annotated as *P. canaliculatum*. A re-examination of the original description of *P. canaliculatum*, however, does not reveal a single character which will identify this description with the tetraploid species rather than with the diploid. The writer is now convinced that *P. canaliculatum* is completely synonymous with *P. biflorum*. It is hoped that anyone making use of her annotations will understand that specimens called "*P. canaliculatum*" are to be considered to be *P. commutatum*.

Although chromosome number is the only completely constant character which separates the two species of the complex, *P. commutatum* is usually distinguished by the greater vigor which often accompanies tetraploidy. These so-called *gigas* characters include a general robustness, a stouter stem, a larger number of leaves and flowers, broader and thicker leaves, coarser peduncles, larger flowers and fruits. *P. commutatum* usually differs from *P. biflorum* in its many-nerved leaves and in having the upper leafy portion of the stem longer than the lower naked portion. The former character occurs in *P. biflorum* var. *melleum;* the latter, in *P. biflorum* var. *necopinum*.

Geographically, *P. commutatum* is found not only over most of the area occupied by *P. biflorum*, but extends in nearly every direction beyond the range of the diploid species. As has previously been pointed out, the present distributions of *P. biflorum* and its varieties suggest that an ancestral diploid once extended at least as far west as the Black Hills of South Dakota. The several areas intervening between the remnants of this diploid have now largely been occupied by the more aggressive tetraploid.

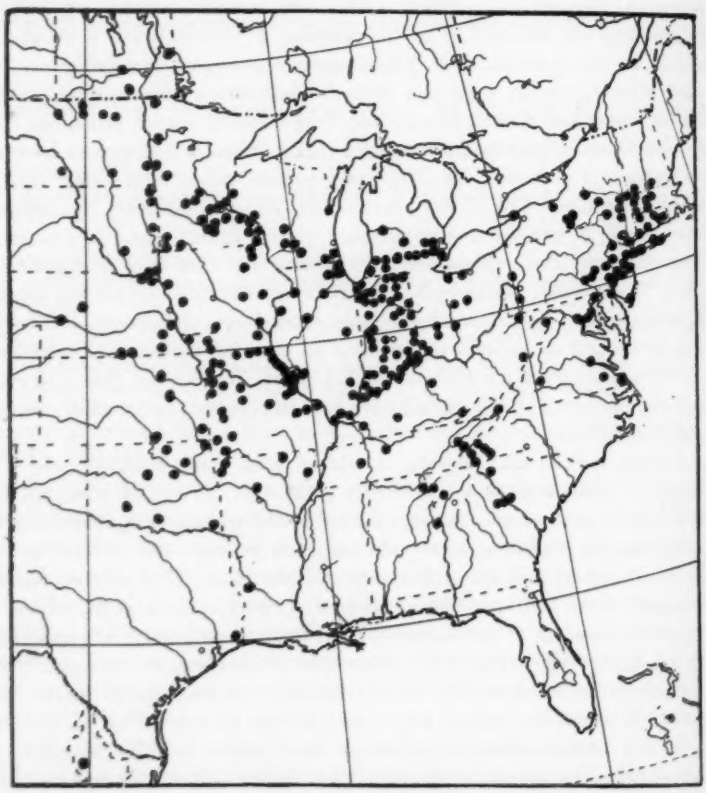
In unusually favorable habitats, in alluvial soils, along roadsides, and when cultivated, *P. commutatum* often reaches great size. It is this ecological type which Fernald[43] in his recent paper separated as the species, disregarding the fact that complete morphological intergradation exists between this extreme and the smaller, more slender ecotype of less favorable situations. The only certain way to distinguish small *biflorum*-like plants of *P. commutatum* growing within the distributional range of *P. biflorum* is by chromosome number. As explained in the section on cytology (page 377), there is no reliable way to estimate chromosome number in *Polygonatum* from herbarium sheets. Such fairly well-correlated characters as general vigor, size of leaves, number of flowers, and stomatal size and distribution, although very useful in this instance, fail to give a complete separation between the diploid and the tetraploid. It is therefore to be expected that the following list of exsiccatae will contain undetected diploids. Especially in the coastal region from New York to Virginia,

[43] Fernald, M. L. Specific distinctions between *Polygonatum biflorum* and *P. canaliculatum*. Rhodora 46:9-12. 1944.

in the mountains of North and South Carolina and Georgia, in Indiana and southern Michigan, the writer found plants which resembled *P. biflorum* except for their large size. Most of these questionable specimens were omitted from the citations of either species, although in most cases the specimens were annotated. It is hoped that the number of errors in citation and annotation will be small.

DISTRIBUTION. In sandy, calcareous, or alluvial soils, woods and open places; generally distributed throughout eastern North America from New Hampshire and Massachusetts, south to Georgia, west to the 102nd meridian from southern Manitoba to northeastern Mexico (Map 3).

ONTARIO. LINCOLN CO.: dry soil, Dimming farm, near Niagara, June 16, 1884, *Macoun* (C). WELLAND CO.: Point Abino, Lake Erie, Aug. 28, 1896, *A. A. A. S. Excursion* (NY); damp ravines, near Stamford, June 12, 1891, *Macoun* (C). ESSEX CO.: Walkerville, June 9, 1891, *Johnson 10455* (Farwell); rich damp woods, Amherstburg, June 11, 1882, *Macoun* (C).



Map 3. Distribution of *Polygonatum commutatum*. Since the map was made, additional specimens from West Virginia, Indiana and Oklahoma have been seen. Based on Goode *Base Map* No. 102. By permission of The University of Chicago Press.

MANITOBA. ST. CLEMENTS DIST.: "Riviere Winipeg," July 14, 1857, *Bourgeau* (G). LAKESIDE DIST.: rich woods, Portage la Prairie, June 10, 1879, *Macoun* (C). MORDEN AND RHINELAND DIST.: by a brook, Morden, Aug. 4, 1896, *Macoun* (C).

NEW HAMPSHIRE. CHESHIRE CO.: Hinsdale, Aug. 2, 1902, *Blanchard 80* (NY), *116* (G).

VERMONT. BENNINGTON CO.: bank of Hoosic River, Pownal, May 30, 31, 1900, *Eggleston 2102* (G).

MASSACHUSETTS. HAMPSHIRE CO.: Southampton, *ex herb. Chapman* (M); bogs, Amherst, July 15, 1875, *Morong* (NY). HAMPDEN CO.: border of woods, slopes above the Connecticut River, Holyoke, Sept. 7, 1926, *Seymour 602* (G, M, NY). BERKSHIRE CO.: Williamstown, June 29, 1901, *Churchill* (G); alluvial riverbank, Sheffield, June 12, 1919, *Churchill* (M); bank of Housatonic River, Stockbridge, June 9, 1912, *Kennedy* (G).

CONNECTICUT. NEW LONDON CO.: railroad grade, Franklin, July 25, 1911, *Woodward* (G). HARTFORD CO.: fence rows, Southington, June 29, 1898, *Andrews 348* (G); dry border of field, Glastonbury, June 10, 1932, *Denslow* (NY); East Hartford, 1900, *Driggs* (G). MIDDLESEX CO.: Chatham, July 5, 1924, *Beals & Chamberlain* (NY). NEW HAVEN CO.: rich soil in copse, Milford, May 31, 1896, *Eames* (US); New Haven, June 5, 1884, *Safford* (US). LITCHFIELD CO.: Canaan, June 10, 1912, *Kennedy* (G). FAIRFIELD CO.: Stratford, July 23, 1871, *ex herb. Day* (NYCP); Fairfield, May 20, 1894, *Eames* (US); shrubby roadside on coast, Westport, Sept. 5, 1928, *Eames 10779* (G); vicinity of Greens Farms, June 7, 1894, *Pollard 41* (US).

NEW YORK. RENSSELAER CO.: Troy, 1828-1834, *Hall* (FM). ALBANY CO.: low moist woods, Wemple, Aug. 4, 1933, *House 20625* (NY). GREENE CO.: Hotaling Island, Hudson River, New Baltimore, Aug. 19, 1909, *Taylor 1395* (NY). DELAWARE CO.: Arkville, July 18, 1915, *Wilson* (NY). ULSTER CO.: Saugerties, May 28, 29, 1910, *Taylor 1904* (NY). ORANGE CO.: Goshen, July 10, 1922, *Denslow* (NY); Tuxedo, June 12, 1892, *Morong* (NY); West Point, May 30, 1906, *Umbach* (NY). ROCKLAND CO.: Piermont, June 2, 1888, *Stabler* (G). BRONX CO.: McLeans Woods, Bronx, May 13, 1913, *Holtzoff* (NY); Bronx Park, May 25, 1896, *Nash 140* (NY). SUFFOLK CO.: Orient, *ex herb. Farlow* (G); East Hampton, Oct. 16, 1919, *Ferguson A-1, A-2* (NY); hilly dry woods, Kings Park, Sept. 8, 1926, *Ferguson 6055, 6056* (NY); openings in oak woods, Roanoke Point, Oct. 4, 1936, *Svenson 8252* (G); copses, Northville, June, 1873, *Young* (FM). NASSAU CO.: Woodmere, June 11, 1916, *Bicknell 560* (NY); dry level oak woods, Seaford, June 11, 1927, *Ferguson 5606* (NY); dry oak woods, south edge of Hempstead Plains, East Meadowbrook, June 20, July 29, 1927, *Ferguson 5650, 5940-a, 5940-c* (NY); Inwood, June 10, 1888, *Poggenburg* (NY). QUEENS CO.: Queens, May 30, 1913, *Bicknell 558a* (NY); Springfield, Aug. 4, 1919, *Ferguson* (NY); Rosedale, July 27, 1926, *Ferguson 5049* (NY); College Point, Sept., 1879, *Schrenk* (NY). RICHMOND CO.: Giffords, Staten Island, May 19, 1889, *Britton* (NY); Staten Island, June, 1868, *ex herb. Crooke* (NY). OTSEGO CO.: alluvial soil, open woods, banks of Cattaraugus Creek, Colliers, July 24, 1927, *Johnson* (NY). ONEIDA CO.: banks of Mohawk River, Utica, June 4, 1904, *Haberer 922* (G). WAYNE CO.: Lyons, 1871, *Hankenson* (NY). TOMPKINS CO.: alluvial soil, Negundo Woods, Ithaca, July 6, 1920, *Muenscher & Bechtel 114* (US, WS); valley of Inlet, Ithaca, June 24, 1915, *Thomas 3751* (G); rich soil, corner of West Danby and Newfield state roads, Ithaca, June 11, 1919, *Wiegand 11789* (M). SCHUYLER CO.: Cayuta Shops Flat, June 17, 1887, *Millspaugh* (FM). CHEMUNG CO.: banks of large streams, without locality, June 11, 1894, *Lucy 2643* (FM).

NEW JERSEY. SUSSEX CO.: Montague Tp., July 16, 1909, *Nash* (NY); Franklin, July, 1875, *Rusby* (UM); Peters Valley, June 1, 1895, *Van Sickle* (US). WARREN CO.: alluvial woods, Delaware River, Belvidere, June 5, 1921, *Mackenzie* (NY). BERGEN CO.: woods, Schraalenburgh, June, 1890, *Cuthbert* (UF); Carlstadt, June 1, 1884, *Niederer* (NYCP). HUDSON CO.: hills back of Hoboken, July, 1847, *without collector* (NY). ESSEX CO.: Millburn, Aug. 4, 1891, *Lighthipe* (NY). MIDDLESEX CO.: near Milltown, near New Brunswick, July 29, 1890, *Vail* (NY). MONMOUTH CO.: Pine Brook road, 2 or 3 mi. s. of Eatontown, Sept. 3, 1923, *Beals, Bassett & Sluyter* (G). BURLINGTON CO.: Kinkora, Aug. 18, 1910, *Taylor 2544* (NY). CAPE MAY CO.: Avalon, June 15, 1925, *Leeds* (M). COUNTY NOT DETERMINED: S. Holland, July 18, 1914, *Miller 1557* (NY).

PENNSYLVANIA. BUCKS CO.: George School woods, June 2, 1906, *Eves* (M); woods, 2½ mi. w. of Durham, Springfield Tp., Aug. 13, 1933, *Witte* (RM). MONTGOMERY CO.: without locality, *ex herb. Martindale* (G). PHILADELPHIA CO.: Philadelphia, *Morong* (M). DELAWARE CO.: meadows, without locality, June, 1861, *ex herb. Canby* (NYCP); moist soil, Chester Heights, Aston Tp., July 31, 1914, *Pennell 1613* (NY); Crum Creek, near Philadelphia, June 7, 1870, *Redfield 8187* (M). CHESTER CO.: without locality, June 5, 1882, *Fergus* (FM); Spread Eagle, June, 1870, *Martindale* (US). BERKS CO.: wooded hill, Moselem Springs, July 4-8, 1915, *Britton* (NY). LANCASTER CO.: Conewago, May, 1889, *Eby* (M); Reinholdsville, Aug. 26, 1889, *Small* (FM). BUTLER CO.: alluvial thickets along Connoquenessing Creek, Ribold, Sept. 18, 1932, *Bright 7761* (Minn), June 28, 1936, *13702* (WS). WASHINGTON CO.: rich woodlands along Mingo Creek, Old Distillery Station, May 28, 1938, *Bright 16324* (WS). COUNTY NOT DETERMINED: meadows, Avondale, June, 1896, *ex herb. Canby* (NYCP).

DELAWARE. NEW CASTLE CO.: New Castle, 1886, *ex herb. Tatnall* (G).

MARYLAND. HARFORD CO.: Spesutie Island, May 26, 1879, *Smith* (US). ANNE ARUNDEL CO.: without locality, May 29, 1878, *Smith* (US). PRINCE GEORGES CO.: between Seabrook and Buena Vista, May 31, 1915, *Maxon 6142* (US); wet woods along Sligo Branch, near the mouth, May 27, 1915, *Standley 11585* (US). MONTGOMERY CO.: Glen Echo, May 19, 1895, *Pollard 261* (US); damp woods, n. of Chevy Chase Lake, May 30, 1911, *Standley 5976* (US); Garrett Park, June 2, 1895, *Topping* (Minn).

DISTRICT OF COLUMBIA. Vicinity of Washington, June 12, 1878, *Chickering* (C, M); pine woods, Dalecarlia Reservoir, May 23, 1905, *Painter 1309* (M); High Island, May 10, 23, 1877, *Ward* (US); Fort Scott, May 15, 1879, *Ward* (US); Woodley Park, June 25, 1879, Sept. 18, 1880, *Ward* (US); alluvial soil, margin of large island, n. w. of Sycamore Island, May 12, 1918, *Wherry* (G, US).

VIRGINIA. PRINCESS ANNE CO.: rich woods, e. of Little Creek, May 4, 1935, *Fernald & Griscom 4355* (G). SUSSEX CO.: dry sandy hickory and oak woods, Burts, July 24, 25, 1936, *Fernald & Long 6155* (G). HENRICO CO.: Richmond, May 13, 1894, *Churchill* (G); Richmond, *De Chalmot* (US). BEDFORD CO.: banks of streams, without locality, June 5, 1868, *Curtiss* (FM); river bank and low rich woods, without locality, June 1, 1871, *Curtiss* (G). GILES CO.: Salt Pond Mt., June 1, 1890, *Brown, Hogg, Vail, Timmerman, Britton & Britton* (NY). SMYTH CO.: riverside, vicinity of Marion, May 22, 1892, *Britton, Britton & Vail* (NY); bluffs of Middle Fork Holston River, Marion, May 22, 1892, *Small* (FM, M, MS, US TYPE of *P. virginicum* Greene); along Nicks Creek, near base of Pine Glade Mt., June 2, 1892, *Small* (FM); south slope of White Rock Mt., June 21, 1892, *Small* (FM).

WEST VIRGINIA. HAMPSHIRE CO.: Hanging Rock, July 9, 1932, *Frye* (Minn). GREENBRIER CO.: White Sulphur Springs, July 16, 1892, *Brown* (NY). FAYETTE CO.: without locality, May 28, 1892, *Nuttall 788* (WVU). SUMMERS CO.: near Bellpoint, May 9, 1932, *Boone 93* (WVU). MONONGALIA CO.: Warm Hollow, July 8, 1939, *Davis & Davis 2746* (WVU); fence row, The Flats, June 4, 1890, *Millspaugh 162* (NY, WVU); Dents Run, June 5, 1940, *Myers* (WVU). BROOKE CO.: along creek, Schubert farm, June 4, 1942, *Schubert* (WVU). OHIO CO.: damp woods, Nichols Hill, Wheeling, May 23, 1937, *Bartholomew 365* (WVU); near Bethany Pike, Oglebay Park, June 21, 1929, *Strausbaugh* (WVU). WETZEL CO.: Rocky Run, near Pine Grove, June 17, 1931, *Haught 439* (WVU). WIRT CO.: damp shaded bank of Little Kanawha River, ½ mi. above mouth of Reedy Creek, June 23, 1934, *Bartholomew 93* (WVU). CABELL CO.: bank of Guyan River, near junction of Russell Creek, June 19, 1937, *Gilbert 589* (WVU). LINCOLN CO.: Hamlin, May 28, 1933, *Harris* (WVU). WAYNE CO.: Dickson, May 12, 1931, *Gilbert 185* (WVU); Wayne, May 27, 1933, *Harris* (WVU); near Ft. Gay, May 7, 1932, *Lycan 17* (WVU).

NORTH CAROLINA. MADISON CO.: wooded slope, French Broad River, near Hot Springs, Aug. 14, 1924, *Wehmeyer 638* (UM). BUNCOMBE CO.: river banks, Biltmore, May 20, 1896, *ex herb. Biltmore 1298* (Minn, RM, US). POLK CO.: rich woods, Whiteoak Mt., Columbus, July 21, 1921, *Peattie 1002* (G); side of Tryon Range, near Columbus, May 10, 1899, *Townsend* (WS). SWAIN CO.: vicinity of Swayney, Sept. 22, 1913, *Mooney* (US). MACON CO.: deep rich soil bordering water-courses, Highlands, May 25, 1897, *ex herb. Biltmore 1298b* (G, M, NY, US); Lake Satulah Falls, Highlands, June 8,

1901, *Magee* (G).

SOUTH CAROLINA. ANDERSON CO.: damp woods, Gluck Mill, Sept. 4, 1917, *Davis 7194* (M, RM). AIKEN CO.: Aiken, July, 1869, *Ravenel* (US).

GEORGIA. RICHMOND CO.: island in Savanna River, 16 mi. above Augusta, April 27, 1904, *Cuthbert 1090* (UF). MCDUFFIE CO.: woods, 2 mi. w. of Thomson, Sept. 17, 1908, *Bartlett 1417* (UM). COBB CO.: small knob, Kennesaw Mt., May 12, 1934, *Perry & Myers 822* (G, NY). FLOYD CO.: cliffs of the Coosa River, 1872, *Ravenel* (M).

ALABAMA. DEKALB CO.: shaded rocky banks, Lookout Mt., 1900 ft. alt., Hotel de Kalb, Mentone, June 4, 1892, *Mohr* (US). LEE CO.: Auburn, May 8, 1897, *Earle & Baker* (NY).

MICHIGAN. MACOMB CO.: Washington, *Cooley* (MS). OAKLAND CO.: Parkedale Farm and Rochester, various dates, 1912 to 1917, *Farwell 2983, 3473, 3673* TYPE of *P. ellipticum* Farwell, *3674, 3675, 3676, 3677, 3677½, 3678, 3679, 3682* TYPE of *P. canaliculatum* var. *oblongifolium* Farwell, *3683, 3981½, 4236a, 4237a, 4508½* TYPE of *P. biflorum* var. *ovatum* subvar. *ellipsoidale* Farwell (Farwell; several of these numbers also at G and NY, but localities or dates not always corresponding). WAYNE CO.: Detroit, near Mich. So. R. R., June 25, 1871, *ex herb. Boott* (G); woods on Belle Ile, June 8, 1893, *Farwell 1150a* (Farwell TYPE of *P. biflorum* var. *ovatum* Farwell); open dryish fields, Rockwood, June 24, 1916, *Farwell 4234* (Farwell), *4235* (Farwell, G). WASHTENAW CO.: Ann Arbor, June 15, 1860, *Almendinger* (UM); bank of Huron River, w. of Ann Arbor, June 30, 1924, *Erlanson 120* (UM); woods, near Ypsilanti, June 13, 1891, *Farwell 1150* (Farwell); moist wooded hillside, left bank of Huron River, just above city beach, Ann Arbor, Aug. 20, 1924, *Gustafson & Best* (UM); edge of low woods, Nichols Arboretum, Ann Arbor, June 30, 1935, *Hermann 6832-a, 6832-b* (FM, MS), *6832-c* (FM); Cedar Bend, Ann Arbor, July 12, 1915, *LaRue* (UM); Huron River Terr., Ann Arbor, June 7, 1903, *Thomson* (UM); woods, w. of Ann Arbor, June 23, 1838, *ex herb. Thurber* (G); near Ypsilanti, June 15, 1870, *Whitney* (UM). INGHAM CO.: Agricultural College, June 16, 1887, *Cooley* (MS); bank of Red Cedar River, Agricultural College, June 26, 1895, *Skeels* (MS); moist open woods, Lansing, June 7, 1917, *Yuncker 184* (US). JACKSON CO.: 3 mi. e. of Hanover, June 28, 1937, *Anderson & Peck* (WS). CALHOUN CO.: s. of Marshall, Aug. 2, 1898, *Beal* (MS). KENT CO.: Grand Rapids, June 27, 1892, July 7, 1893, *Bailey* (UM); Grand Rapids, June, 1886, *Crozier* (NY, US); Grand Rapids, Aug. 21, 1935, *Rusby* (NY). KALAMAZOO CO.: shady spot, roadside, Schoolcraft, June 6, 1903, *Burgess 55* (FM); in lane leading to lake, Sugarloaf Lake, June 16, 1903, *Burgess 155* (FM); roadside, Schoolcraft, Sept. 30, 1903, *Burgess 397* (FM); fence row, Sugarloaf Lake, Oct. 3, 1903, *Burgess 460* (FM). ST. JOSEPH CO.: between Mud Lake and Clear Lake, June 27, 1937, *Anderson* (WS); Constantine, June 9, 1903, *Davis* (WS). VAN BUREN CO.: South Haven, July 6, 1910, *Pennington* (UM); wooded bank, Keeler, 1906, *Pepoon 763* (MS). BERRIEN CO.: flood plain, Warren Woods, May 18, 1921, *Billington* (UM).

OHIO. WAYNE CO.: Wooster, July 4, 1907, *Laughlin 970* (G). LORAIN CO.: woods, Oak Point, June 8, 1895, *Ricksecker* (US). ERIE CO.: Cedar Point, May 29, 1894, *Moseley* (M). RICHLAND CO.: waste ground, without locality, June 20, 1892, *Wilkinson* (Minn). FRANKLIN CO.: Columbus, May 30, 1898, *Colevenger* (US). CHAMPAIGN CO.: near Urbana, June 23, 1838, *without collector* (UM). CLARK CO.: Springfield, *Williams* (M). BUTLER CO.: moist woods, Oxford, June 22, 1910, *Overholts* (M). HAMILTON CO.: edge of woods, Mt. Airy Forest, Cincinnati, June 8, 1931, *Stephenson* (RM).

INDIANA. STEUBEN CO.: middle of high wooded black oak slope, north side of Cheeseboro Lake, S. 19, 3½ mi. n. w. of Angola, June 22, 1937, *Deam 57888* (D); woods, near Lake Gage, June 16, 1903, *Deam* (D). LAGRANGE CO.: white oak woods, 3 mi. e. of Howe, June 5, 1915, *Deam 15911* (D); woods, north side of Cedar Lake, June 12, 1916, *Deam 20180* (D); base of sandy black oak slope, 1 mi. s. of Mongo, Sept. 14, 1918, *Deam 26335* (D); black and white oak woods, 1⅛ mi. s. e. of Mongo, July 13, 1923, *Deam 39093* (D); in sphagnum, tamarack bog along Pigeon River, 1½ mi. s. e. of Mongo, June 17, 1937, *Deam 57860* (D). NOBLE CO.: dry woods, 4 mi. s. e. of Ligonier, June 26, 1914, *Deam 14346* (D); moist woods, 5 mi. s. w. of Albion, Aug. 25, 1914, *Deam 14697* (D); sandy soil, school-house grounds, north side of Blackman Lake,

1 mi. e. of Kimmel, July 1, 1924, *Deam 40789* (D). WHITLEY CO.: black and white oak woods, north side of New Lake, 9 mi. n. w. of Columbia City, July 1, 1924, *Deam 40779* (D). ADAMS CO.: without locality, Aug. 1, 1900, *Kauffmann* (UM). HUNTINGTON CO.: bank of Salamonie River, 3 mi. n. w. of Warren, Aug. 15, 1924, *Deam 40948* (D). JAY CO.: woods, Godfrey Indian Reserve, S. 20, 3 mi. n. w. of Pennville, June 11, 1931, *Deam 50258* (D). DELAWARE CO.: river bank, 1 mi. e. of Eaton, June 4, 1911, *Deam 8532* (D). WAYNE CO.: woods, 3½ mi. n. w. of Richmond, June 4, 1913, *Deam 13136* (D). UNION CO.: wooded ravine, 3 mi. s. of Liberty, June 16, 1915, *Deam 16006* (D). DECATUR CO.: along a fence along a woods, 5 mi. s. of Greensburg, May 31, 1921, *Deam 34171* (D). DEARBORN CO.: wooded ravine, ½ mi. w. of Aurora, June 17, 1915, *Deam 16038* (D); wooded bank of Laughery Creek, 4 mi. w. of Aurora, June 18, 1915, *Deam 16109* (D). RIPLEY CO.: wooded hillside along Laughery Creek, just e. of Versailles, July 23, 1913, *Deam 13789* (D). JENNINGS CO.: wooded area, 5 mi. s. e. of Vernon, May 22, 1942, *Friesner 16681* (WS). SWITZERLAND CO.: wooded hillside, just n. of Vevay, July 25, 1913, *Deam 13824* (D). JEFFERSON CO.: Hanover, June 17, 1874, *Coulter* (FM). CLARK CO.: without locality, May 6, 1851, *Mohr* (US). ELKHART CO.: woods, river bank, 1½ mi. n. of Middlebury, June 4, 1912, *Deam 10966* (D). MARSHALL CO.: Long Point, near Lake Maxinkuckee, June 17, 1901, *Clark 1774* (NY, US); woods, south side of Lake Maxinkuckee, Sept. 14, 1921, *Deam 34769* (D); Lake Maxinkuckee, Aug. 8, 1899, *Evermann 950* (US). FULTON CO.: woods along Tippecanoe River, just n. of DeLong, June 7, 1920, *Deam 30982* (D). MIAMI CO.: border of woods, 1 mi. n. w. of Denver, June 30, 1922, *Deam 36797* (D). GRANT CO.: woods, 2 mi. n. e. of Van Buren, June 16, 1907, *Deam 2049* (D). JACKSON CO.: slope of wooded beech ravine, 1 mi. w. of Medora, July 15, 1919, *Deam 28129* (D). FLOYD CO.: base of wooded slope, 2 mi. w. of New Albany, June 13, 1919, *Deam 27931* (D). HARRISON CO.: near base of wooded slopes, Falling Springs Hollow, 3 mi. e. of Elizabeth, June 1, 1917, *Deam 23336* (D). STARKE CO.: black oak woods, 6 mi. n. e. of North Judson, June 27, 1930, *Deam 49007* (D). PULASKI CO.: wooded bank, Tippecanoe River, 3½ mi. n. e. of Winamac, June 9, 1923, *Deam 38831* (D). WHITE CO.: black oak clearing, 2½ mi. s. of Lee, Sept. 17, 1921, *Deam 34906* (D). TIPPECANOE CO.: woods, 1½ mi. n. e. of Romney, May 25, 1922, *Deam 36063* (D). BOONE CO.: roadside, 4 mi. n. of Lebanon, June 19, 1943, *Friesner 17749* (WS). HENDRICKS CO.: wooded creek bottom, White Lick River, June 22, 1912, *Deam 11236* (D). PUTNAM CO.: woods, 2 mi. s. w. of Morton, Aug. 24, 1922, *Deam 37821* (D); Greencastle, May, 1893, *Underwood* (NY). MORGAN CO.: low wooded bank, White River, 1¼ mi. s. e. of Paragon, May 21, 1922, *Deam 35866* (D). MONROE CO.: near "Phi Delt" house, Bloomington, June 7, 1923, *Hawkin* (UF). GREENE CO.: along railroad, ½ mi. e. of Bushrod, May 26, 1912, *Deam 10682* (D). LAWRENCE CO.: wooded bluff, [East Fork of] White River, ¼ mi. e. of Tunnelton, May 16, 1918, *Deam 24812* (D). DAVIESS CO.: wooded bank, [East Fork of] White River, just e. of the Portersville Bridge, July 17, 1919, *Deam 28221* (D). CRAWFORD CO.: roadside, ½ mi. s. of Marengo, June 7, 1919, *Deam 27777* (D, G); wooded slopes, Grantsburg, June 9, 1919, *Deam 27801* (Farwell). PERRY CO.: wooded bluff, Ohio River, 5 mi. e. of Cannelton, June 29, 1915, *Deam 16626* (D). SPENCER CO.: dry woods, 3 mi. w. of Troy, June 30, 1915, *Deam 16656* (D). WARRICK CO.: high wooded bank, Cypress Creek, 2 mi. e. of Newburg, June 11, 1918, *Deam 25301* (D). PORTER CO.: woodlands, without locality, June 28, Aug. 11, 1929, *Buhl 103* (FM). LAKE CO.: north slope, low wooded dune, ½ mi. e. of East Gary, June 10, 1922, *Deam 36458* (D); sandy wooded ridge, 2½ mi. n. w. of Hobart, July 18, 1931, *Deam 50553* (D); rich woods, Valparaiso, May 23, 1900, *Lansing 824* (FM); dry sandy woods, Clarke, Sept. 3, 1903, *Lansing 1849* (FM). JASPER CO.: black oak sand hill, 5 mi. w. of Gifford, July 14, 1920, *Deam 31706* (D). FOUNTAIN CO.: along creek, near Veedersburg, June 5, 1905, *Deam* (D); on crest of white and black oak ridge, Portland Arch Park, near Fountain, Aug. 15, 1932, *Deam 52835* (D). KNOX CO.: wooded border of Claypool Pond, 15 mi. s. w. of Decker, July 8, 1915, *Deam 17000* (Minn). GIBSON CO.: woods, Gordon Hills, 6 mi. w. of Patoka, July 6, 1915, *Deam 16905* (D). POSEY CO.: wooded ravine, 4 mi. s. of Mt. Vernon, May 24, 1911, *Deam 8322a* (D).

KENTUCKY. HARLAN CO.: top of Big Black Mt., near state line, June 17, 1936, *Camp 1492* (NY). SCOTT CO.: Elkhorn Cliff, Stamping Ground, May 12, 1930, *Singer* (US). WARREN CO.: Bowling Green, June, 1899, *Price* (M). LYON CO.: Kuttawa, June 2-18, 1909, *Eggleston 4579* (NY). COUNTY NOT DETERMINED: moist shady thicket, Elk Lick Falls, May 19, 1923, *McFarland 99* (M, US).

TENNESSEE. SEVIER CO.: rocky ravine, Elkmont, July 29, 1924, *Wehmeyer 378* (UM). KNOX CO.: woods, Knoxville, April, May, 1898, *Ruth 140, 735* (US), *147, 749* (NY), *148, 781* (M). CHEATHAM (?) CO.: limestone of Harpeth River, w. of Nashville, May 17, 1934, *Harger 7807A* (G). HENDERSON CO.: moist sandy hillsides, near Lexington, May 20, 1920, *Palmer 17575* (M).

WISCONSIN. BROWN CO.: DePere, June 23, 1888, *Kellogg* (US); Wrightstown, Aug. 17, 1879, *Schuette* (FM); Bellevue Creek, June 13, 1880, *Schuette* (FM); Fort Howard, June 18, 1881, *Schuette* (G); copses, Fort Howard marsh, June 26, 1886, June 26, 1887, *Schuette* (FM); Kellogg stockfarm, Allouez, June 27, 1897, *Schuette* (FM, NY); Green Bay, June 22, 1898, *Schuette* (FM). RACINE CO.: Racine, Sept. 11, 1879, *Davis* (M). WALWORTH CO.: Lake Geneva, *Ayer* (FM); vicinity of Delavan, July 11, 1919, *Hollister 43* (US); 1½ mi. n. w. of Lake Geneva, 1885, *Scoville* (RM); margin of woods, near Lake Geneva, *Scoville* (RM). DANE CO.: Madison, Aug. 25, 1893, *Churchill* (G). SAUK CO.: woods, Mirror Lake, July 13, 1903, *Eggert* (M). RICHLAND CO.: rich soil, wooded hillside, ½ mi. e. of Richland Center, June 7, 1912, *Lansing 3421* (FM). JUNEAU CO.: Camp Douglas, July 16, 1890, *Mearns 666* (US). BUFFALO CO.: near Fountain City, *Finkelnburg* (Minn). POLK CO.: St. Croix Falls, July 18, 1900, *Baker* (G).

ILLINOIS. LAKE CO.: beach, n. of Waukegan and e. of the glacial Glenwood Ridge, June 16, 1909, *Gates 3025* (UM). COOK CO.: edge of woods, Palos Park, May 24, 1913, *Johnson* (NY); woods, near Chicago, June 30, 1892, June 29, 1891, *Moffatt 171, 329* (Minn); Stony Island, June 25, 1914, *Smith 5932* (G, M). DU PAGE CO.: railroad, Lisle, June 4, 1918, *Martinek 191* (US); woods, Naperville, May 9, 1895, *Umbach* (Minn), May 21, 1895, *Umbach* (US), June 16, 1898, *Umbach 1040* (G). KANE CO.: shaded ground, Bliss Woods, 7 mi. w. of Aurora, July 30, 1925, *Erlanson 1547* (UM). LA SALLE CO.: rich shady woods, Starved Rock, June 1-7, 1909, *Greenman, Lansing & Dixon 9* (G, NY). PEORIA CO.: moist woods, Peoria, June, 1904, *McDonald* (G). ROCK ISLAND CO.: Port Byron, Aug. 11, 1892, *ex herb. Harper* (WS). HENDERSON CO.: moist shaded sand dunes, Oquawka, July 7, 1908, *Gleason* (G). CHAMPAIGN CO.: shady bank, Crystal Lake, Urbana, May 23, 1911, *Pease 13090* (G). RICHLAND CO.: near Bird Haven, 2½ mi. n. of Olney, May 10, 1910, *Ridgway* (US); Larchmound, Olney, May 20, 1919, *Ridgway 807* (G). WHITE CO.: wooded hillsides, Grayville, June 22, 1919, *Palmer 15575* (M). POPE CO.: rocky hillside woods, Golconda, June 5, 1919, *Palmer 15367* (M). JOHNSON CO.: rocky hillside woods, Vienna, Apr. 28, 1919, *Palmer 14984* (M). ALEXANDER CO.: low rich woods, Olive Branch, May 10, 1919, *Palmer 15098* (M). ST. CLAIR CO.: Carondelet, Sept. 4, 1891, *Douglass* (M).

MINNESOTA. HOUSTON CO.: sandy soil, hillside, Spring Grove, June 5, 1902, *Rosendahl 351* (Minn); Winnebago Valley, June 12, 1899, *Wheeler 184* (Minn). WINONA CO.: Winona, June, July, 1912, *Freiberg* (M); dry sandy soil and stony side of bluffs, without locality, June, 1886, *Holzinger* (Minn). WABASHA CO.: woods, Lake City, May, 1881, *Hammond 43* (Minn); near Lake City, June 14, 1883, *Manning* (Minn). OLMSTEAD CO.: Rochester, Lat. 44, June 17, 1902, *Ainslie 1040* (Minn). GOODHUE CO.: Cannon Falls, May, 1881, *Sandberg* (Minn). RAMSEY CO.: St. Paul, June 20, 1899, *ex herb. Moore & Moore* (RM). HENNEPIN CO.: rich woods, near Minneapolis, June, 1892, *Burglehaus* (Minn, MS); Lake Harriet, Sept. 15, 1896, *Heller* (Minn); Minneapolis, June 13, 1877, June, 1878, *Herrick* (Minn); Minneapolis, June, 1878, *Kassube* (Minn); Fort Snelling, June 9, 1891, *Mearns* (US); Fort Snelling Reservation, June 19, 1909, *Rosendahl 2132* (Minn); Minneapolis, June, 1895, *Sheldon* (Minn). CARVER CO.: Chaska, June, 1891, *Ballard 67, 69* (Minn). RICE CO.: Northfield, 1912, *without collector G. 139* (Minn). LE SUEUR CO.: Elysian, June, 1891, *Sheldon 41* (Minn); Elysian, June, 1891, *Taylor 34* (Minn). NICOLLET CO.: Middle Lake, June, 1892, *Ballard 969* (Minn). WASECA CO.: Janesville, June, 1891, *Taylor 118a, 262* (Minn). BLUE EARTH CO.: Madison Lake, June,

1891, *Sheldon 116* (Minn). STEARNS CO.: St. Cloud, June, 1897, *Campbell* (FM, Minn). MEEKER CO.: Litchfield, June, 1892, *Frost* (Minn). KANDIYOHI CO.: Willmar, June, 1912, *without collector 89* (Minn). ROSEAU CO.: Oak Point, July, 1894, *MacMillan & Sheldon 1098* (Minn). POLK CO.: Crookston, Aug., 1900, *MacMillan & Skinner* (Minn). CLAY CO.: rich woods, Moorhead, June 18, 1929, *Solheim 205* (RM). OTTERTAIL CO.: Battle Lake, Aug., 1892, *Sheldon 3357* (Minn). JACKSON CO.: vicinity of Heron Lake, June 10, 1902, *Skinner 45* (Minn). PIPESTONE CO.: Pipestone, June, 1895, July, 1896, *Menzel* (Minn). ROCK CO.: at base of mound, Luverne, Sept. 10, 1901, *Wheeler 1068* (Minn).

IOWA. WINNESHIEK CO.: rich woods, without locality, June 18, 1895, *Fitzpatrick & Fitzpatrick 2643* (G). FAYETTE CO.: wooded hillsides, Fayette, July, 1893, *Fink* (G); rocky hillside, without locality, June 28, 1894, *Fink 572* (US). BLACKHAWK CO.: Snag Creek woods, June 14, 1929, *Burk 343* (M); clay soil, Cedar Falls, July 7, 1926, *Pammel 263* (G, M); sandy soil, woods and islands of Cedar River, Island Y.M.C.A. Camp, Cedar Falls, July 9, 1925, *Pammel 663* (G). JOHNSON CO.: woods, without locality, June 13, 1900, *Fitzpatrick & Fitzpatrick* (D); Iowa City, *Hitchcock* (M). POWESHIEK CO.: Grinnell, 1886, *Norris* (M). VAN BUREN CO.: rich woods, Bentonsport, June, 1920, *Graves 1719* (M); Stockport, June, 1925, *Graves 2055* (M). DECATUR CO.: moist woods, Decatur, June 29, 1904, *Anderson* (RM); low rich woods, without locality, June 6, 1898, *Fitzpatrick & Fitzpatrick* (FM, RM). SHELBY CO.: without locality, May 30, 1894, *Fitzpatrick & Fitzpatrick* (M, MS). WOODBURY (?) CO.: ravines, "Sargent's hill" [Sargeant Bluff?], June, 1853-54, *Hayden* (M).

MISSOURI. SCOTLAND CO.: woods, north side of Wyaconda River, near Azen, June 30, 1933, *Palmer & Steyermark 40982* (M, NY); along North Fork of Fabius River, w. of Memphis, June 30, 1933, *Palmer & Steyermark 41000, 41001* (M). MARION CO.: Hannibal, May, 1906, Aug. 1, 1914, June 20, 1915, *Davis 1200, 3105, 6588* (M); Scipio, July 24, 1915, *Davis 4775* (M); church-yard slopes, Withers Mill, July 14, 1917, *Davis 7545* (M). SHELBY CO.: near Bethel, June 29, 1933, *Palmer & Steyermark 40914* (M). MACON CO.: Ethel, June 12, 1915, *Bush 7622* (M). LINN CO.: without locality, May 30, 1937, *Crookshanks 15* (M). RALLS CO.: Ilasco, Aug. 20, 1911, *Davis 987* (M); Bear Creek bluffs, near Oakwood, June 2, 1916, *Davis 1290* (M); near New London, June 27, 1933, *Palmer & Steyermark 40716* (M). PIKE CO.: Norris farm, near Eolia, Aug. 26, 1916, *Davis* (M, Minn). LINCOLN CO.: Silex, May 29, 1915, *Davis* (M). ST. CHARLES CO.: Gilmore, May 26, 1917, *Davis 7372* (M). ST. LOUIS CO.: rich woods, Allenton, May 20, 1918, *Churchill* (G); Allenton, May 26, 1886, *Eggert* (M); Jefferson Barracks, *Eggert* (M); Ramona Park, June 8, 1907, *Fullgraf* (M); near St. Louis, June 20, 1892, *Glatfelter* (UM); Windsor Springs, July 1, 1890, *Hitchcock* (M); Jefferson Barracks, July 6, 1890, *Hitchcock* (M); Meramec Highlands, July 29, 1905, *Johnson* (M); Allenton, June 8, 1903, *Kellogg* (M); Allenton, June, 1902, *Letterman* (M, US); Allenton, Aug. 13, 1933, *Lodewyks 27* (M); Creve Coeur Lake, July 20, 1894, *Misch* (M); Meramec Highlands, May 23, 1897, *Norton & Ferguson* (M); St. Louis, July, Aug., 1891, *Trelease* (M). FRANKLIN CO.: Gray Summit, May 19, 1928, *Greenman 4545* (M); Gray Summit, May 25, 1927, *Kellogg 830* (M); St. Albans, June 5, 1930, *Kellogg 15144* (M); in shade, moist hillside, Pacific, May 15, 1921, *Payson 2460* (RM). JEFFERSON CO.: in moist rich shady soil, Antonia, May 30, 1937, *Barkley 1149* (M, WS); woods, near Victoria, Aug. 24, 1892, *Eggert* (M); Selma, May 30, 1923, *Greenman 4283* (M); Victoria, Aug. 7, 1890, *Hitchcock* (M); Kimmswick, June 7, 1885, *Wislizenus 414* (M). WASHINGTON CO.: woods, near Mineral Point, May 29, 1892, *Eggert* (M). PERRY CO.: 1 mi. n. of Menfro, July 30, 1934, *Steyermark 14041* (M). MADISON CO.: Mine La Motte, May 19, 1927, *Greenman* (M). IRON CO.: along railroad, near Vulcan, May 6, 1908, *Smith 311* (FM); woods, Des Arc, May 12, 1908, *Smith 380* (FM); Ironton, June 18, 1897, *Savage & Stull 197* (FM). WORTH CO.: 1 mi. s. of Denver, Aug. 30, 1934, *Steyermark 15053* (M). GENTRY CO.: low woods, along East Fork of Grand River, 3 mi. n. w. of Albany, Aug. 29, 1934, *Steyermark 15014* (M). ATCHISON CO.: Watson, June 1, 1894, *Bush 527* (M). CALDWELL CO.: 6 mi. n. of Cowgill, Aug. 26, 1934, *Steyermark 14884* (M). CLINTON CO.: 6 mi. s. of Cameron, Aug. 27, 1934, *Steyermark 14918* (M). CLAY CO.: without locality, July 18, 1933, *Bush 12690* (M). JACKSON

CO.: Independence, June 7, 1894, *Bush 533* (M); prairies, Lake City, June 2, 1915, *Bush 7565* (G, M, NY, US); Courtney, June 7, 8, 17, 1917, *Bush 7996* (M), *7996A* (NY), *8000* (M, US), *8000A* (NY, US), *8002* (M); Swope Park, June 9, 1917, *Hoffmann* (M). JOHNSON CO.: rich woods, near Columbus, June 22, 1930, *Palmer 36717a* (M). CASS CO.: without locality, June 9, 1864, *Broadhead* (M). COOPER CO.: Otterville, May 19, 1936, *Bush 15523* (M). MORGAN CO.: low slopes, along Procter Creek, July 7, 1934, *Steyermark 13194* (M). PHELPS CO.: Jerome, May 28, 1914, *Kellogg 537* (M). ST. CLAIR CO.: Osceola, July 28, 1933, *Bush 12804* (M). CEDAR CO.: n. of Bear Creek P. O., July 16, 1934, *Steyermark 13548* (M). GREENE CO.: Springfield, June 7, 1903, *Standley* (US); vicinity of Springfield, June 15, 1907, *Standley* (US); along railroad, s. e. of Springfield, Aug. 29, 1911, *Standley 8392* (US); thin woods, vicinity of Strafford, Aug. 27, 1912, *Standley 9499* (US). JASPER CO.: Webb City, June 14, 1903, *Palmer 735* (M); low rich woods, Neck City, Aug. 16, 1919, *Palmer 15872* (Farwell); Webb City, Aug. 18, 1919, *Palmer 15922* (Farwell); near Reeds, June 2, 1924, *Palmer 25259* (M). BARRY CO.: Flat Creek, May 19, 1936, *Bush 15513* (M).

ARKANSAS. CRAIGHEAD CO.: Jonesboro to Lake City, July 5, 1927, *Demaree 3582* (M). FULTON CO.: Mammoth Spring, June 1, May 14, 1924, *Wheeler 14, 37* (FM). FAULKNER CO.: Arkansas River, 7 mi. w. of Conway, May 30, 1923, *Wheeler 79* (FM). CARROLL CO.: Eureka Springs, May 15, 1914, *Palmer 5624* (M). WASHINGTON CO.: near Farmington, May 4, 1925, *Palmer 26987* (M).

LOUISIANA. NATCHITOCHES PARISH: sandy hillside woods, Chopin, April 21, 1915, *Palmer 7335* (M, NY, US).

NORTH DAKOTA. RAMSAY CO.: moist woods, Devils Lake, July 1, 1905, *Lunell 286* (Minn). BENSON CO.: thickets, Peninsula of Lake Ibsen, Aug. 15, 1906, *Lunell 286*, Aug. 27, 1909, *701* (Minn), Sept. 3, 1914, *1232* (Minn TYPE of *P. commutatum* var. *lineamentosum* Lunell, NY). BOTTINEAU CO.: prairies, Willow City, June 20, 1889, *Lunell* (RM). MCHENRY CO.: Towner July 21, 1908, *Lunell* (NY). WARD CO.: rich alluvial soil, river bank near picnic grounds, Oak Park, Minot, June 21, 1929, Sept. 2, 1929, *Lakela 173* (Minn). CASS CO.: banks of Red River, Fargo, Sept. 29, 1933, *Nelson & Nelson 1019* (RM). LAMOURE CO.: open woods, Adrian, June 27, 1912, *Bergman 1822* (Minn). MORTON CO.: without locality, July 5, 1906, *Bell 296* (M).

SOUTH DAKOTA. ROBERTS CO.: rich woods, Coulee, July, 1922, *Over 14332* (US). GRANT CO.: Big Stone, Aug., 1894, *Williams* (RM). BROOKINGS CO.: Lake Oakwood, *Griffiths* (M); shady banks, Lake Hendricks, June 11, 1898, *Hepner* (RM); damp woods, Oakwood, May 23, 1902, *Johnson* (M); Warren woods, Brookings, June 11, 1898, *Lawrence* (WS); Brookings, Aug., 1924, *Moore 1562* (Minn); Lake Campbell, Aug., 1924, *Moore 1569* (Minn). HANSON CO.: Alexandria, May 11, 1911, *Weber* (UF). UNION CO.: thickets, Brule Creek, June 27, 1921, *Over 13682, 13683* (US). CLAY CO.: woods, Vermillion, May 22, Aug. 1, 1911, *Visher 4018* (FM, M), June 28, 1910, *4167* (M).

NEBRASKA. DIXON CO.: Ponca, June 14, 1893, *Clements 2545* (G, Minn, US). CEDAR CO.: St. Helena, *Bruhin* (M). CASS CO.: South Bend, May 12, 1900, *Hedgcock* (M). LANCASTER CO.: s. w. of Lincoln, June 5, 1900, *Hedgcock* (M); Lincoln, Aug., 1889, *Webber* (M, NY). GAGE CO.: moist woods, Beatrice, June 13, 1899, *Washburn* (US). NUCKOLLS CO.: without locality, July, Aug., 1899, *Hedgcock* (M). WEBSTER CO.: Red Cloud, June 8, 1904, *Bates 3212* (Minn). THOMAS CO.: hillside, Middle Loup River, near Norway, June 22, 1893, *Rydberg 1408* (US); dry hillside, near Plummer Ford, Dismal River, July 5, 1893, *Rydberg 1483* (G, NY, US). LINCOLN CO.: Hershey, June 11, 1903, *Mell 98* (US).

KANSAS. CRAWFORD CO.: 6 mi. s. e. of Pittsburg, June 21, 1929, *Rydberg & Imler 165* (NY). RILEY CO.: Prospect Hill, near Manhattan, Sept. 28, 1923, *Nelson* (M); Manhattan, Aug. 26, 1892, *Norton* (C); woods, without locality, 1896, *Norton 834* (G, M, NY, RM, US); Manhattan, Aug. 19, 1892, *Thompson* (M). LYON CO.: wooded hillsides, without locality, May 29, 1895, *Chamberlin* (WS). COWLEY CO.: without locality, June, 1898, *White* (M).

OKLAHOMA. OTTAWA CO.: moist woods, near Ottawa, Aug. 29, 1913, *Stevens 2506* (G, Minn). ROGERS CO.: Catoosa, May 14, 1895, *Bush 1282* (M). OSAGE CO.: on shady wooded creek bank, near Pawhuska, Aug. 9, 1913, *Stevens 1999* (G, M, Minn, US).

PAYNE CO.: sandy wet soil, 2 mi. n. of Ripley, June 29, 1935, *Dillingham* (WVU). CREEK CO.: Sapulpa, July 27, 1894, *Bush 578* (M). LOGAN CO.: shady hillside, Cimmaron Bluffs, near Guthrie, June 14, 1914, *Stevens 3292* (G). MCCURTAIN CO.: near Shawneetown, Aug. 13, 1853, *Bigelow* (US); Boggy Creek, Shawneetown, *Bigelow* (NY). MURRAY CO.: Platt National Park, Oct. 31, 1935, *Merrill & Hagan 1691* (FM). COMANCHE CO.: vicinity of Fort Sill, May 20, 1916, *Clemens 11532* (M, RM). COUNTY NOT DETERMINED: chiefly on the False Washita, between Fort Cobb and Fort Arbuckle, 1868, *Palmer 325* (NY, US).

TEXAS. HARDIN CO.: 7¾ mi. w. of Silsbee, Village Creek, Oct. 6, 1934, *Cory 11169* (G).

MEXICO. NUEVO LEON: Mesa Canyon, mountains near Monterrey, July, 1933, *Mueller & Mueller 339* (G, FM).

UNIDENTIFIED SPECIES

Convallaria hirta Bosc ex Poiret in Lamarck, Encyc. Méth. Bot. 4:369. 1797.

Polygonatum hirtum Pursh, Fl. Am. Sept. 1:234. 1814.

No species conforming to the original description of *Convallaria hirta* is known from North America.

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